University of Alberta

Forest Productivity in Naturally Saline Landscapes of Alberta's Boreal Forest

by

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Dedication

Dedicated to Marjory, Wally, Don, and Ruth Mary
My favorite grandparents

Abstract

The effect of salinity on boreal forest plants is of growing concern today because oilsand mining in northern Alberta produces large areas of salt-affected soils that need to be reclaimed. We examined the soil and vegetation characteristics of seven naturally saline forested sites in northern Alberta to better understand the effect of soil salinity on mature boreal forest plants. Soil salinity, sodicity, pH, nutrients, moisture content, and temperature were measured in high, medium, and low salinity soils; salt ions, nutrients, and carbon and nitrogen stable isotope ratios were measured in aspen and white spruce foliage. Both tree height growth and basal area growth were determined. Aspen growth decreased with increasing salinity, but white spruce growth seemed to be more strongly affected by environmental factors other than salinity. Both species appeared to be robust against nutritional toxicities and deficiencies commonly encountered in saline soils, indicating a tolerance for some saline conditions.

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Symbols, abbreviations, and definitions

Symbols and abbreviations

ANOVA – analysis of variance
AWHC – available water holding capacity
b – the intercept of the equation for a line
BAI – basal area increment
BH Age – breast height age
CEC – cation exchange capacity
DBH – diameter at breast height
EC – electrical conductivity
ESR – exchangeable sodium ration
K_G – Gapon exchange constant
PGM – parent geological material
P_{CO2} – partial pressure of carbon dioxide
R – the abundance ratio of a heavier to lighter isotope
SAR – sodium absorption ratio = $[Na^+]/\sqrt{([Ca^{2+}] + [Mg^{2+}])}$; [ ] in mg/L
SI – site index
θ – soil volumetric water content or soil moisture content

Definitions

Soil salinity ranges measured in a saturation extract:
Non saline – EC < 2 dS/m
Slightly saline – EC = 2-4 dS/m
Moderately saline – EC = 4-8 dS/m
Highly saline – EC = 8-16 dS/m
Extremely saline – EC > 16 dS/m

Sodic – SAR ≥ 13
Alkaline – pH > 7.0
Highly alkaline – pH > 8.5

Field capacity (soil water potential of 0.1 for sandy soils or 0.3 atm for finer textured soils)
Wilting point (soil water poten of 15 atm)

LCCS – land capability classification system for aspen, white spruce, and jackpine dominated forests in the oilsands region (Leskiw 2004, 2006)
LCCS Class 1 – high capability (median SI = 20.8 m)
LCCS Class 2 – moderate capability (median SI = 18.4 m)
LCCS Class 3 – low capability (median SI = 16.0 m)
LCCS Class 4 – conditionally productive (median SI = 13.5 m)
LCCS Class 5 – non-productive (median SI = 11.1 m)

Chapter 1. Introduction

1.1. Saline soils

Terrestrial life on earth depends upon a thin layer of material at the earth's surface, the soil, a material created over time by interactions among organisms, climate, topography, and rock (Jenny 1941). Soil quality is critical to the growth of plants and the sustenance of human life; the deterioration of soils has been linked to the collapse of past civilizations, most notoriously of the Sumerians (Jacobsen and Adams 1958). Soils control the provision of water and nutrients to plants, thus regulating their productivity. Plants can endure multiple stresses, and many species have adapted to less favorable soil conditions, but harsher conditions usually mean reduced growth. To create favorable conditions for plant growth, one stress that humans commonly alleviate is drought stress. Unfortunately, by manipulating water in the environment, humans often introduce a factor that interferes with plant water uptake – salinity – it was salinization from irrigation and land conversion that destroyed Sumerian soils (Jacobsen and Adams 1958). Thus, the responses of plants to salinity stress have been relevant to humans since the dawn of agriculture.

Soil salinization is not only caused by agricultural manipulation of the environment. Industrial activities such as drilling and mining for oil and gas can also be a source of excess salts which cause soil salinization. In Canada's boreal forest, oilsands mining in the Athabasca oilsands region near Fort McMurray, Alberta, is a major industrial source of salt affected soils. A sodium hydroxide slurry is used to extract bitumen from oilsands and the process waters are recycled over and over, leading to highly saline and sodic oilsand tailings (FTFC 1995). Gypsum can be added to consolidate these tailings, leading to even higher salt concentrations (FTFC 1995). A second source of saline material from oilsand mining is the naturally saline marine shale overburden (FTFC 1995), which is dug through to reach the oil sand deposits. Once exposed, the salts in this material can leach into the groundwater and move into adjacent soils. Due to these sources of salts, a large area of the post-mined landscape is expected to be affected by salinity, posing multiple reclamation challenges. Because of the magnitude of the disturbance and the reliance of local communities on the boreal forest for food, fiber, water, and other values, the responses of boreal forest plants to salt stress have become very relevant to Canadians in recent years.

Little is known about the effect of salinity on boreal forest communities and ecosystems, or even if boreal forests can establish on saline soils. Lieffers (1984) found that emergent vegetation community composition in boreal lakes was strongly affected by lake water salinity, and Burchill and Kenkel (1991) found that herbaceous and shrub community composition at boreal salt pans was also strongly affected by salinity, but neither examined forest vegetation. Several studies have documented significant damages on boreal forest vegetation caused by brine spills (Rowell and Crepin 1977, Edwards and Blauel 1975). Research along the Tanana River in Interior Alaska has found forests growing on salt

affected soils (Yarie et al. 1993), but the highest salinity levels examined were below what is expected after oilsands mining. The most recent research in this area was a study on naturally saline communities of northern Alberta by Purdy et al. (2005), who documented that boreal forest trees can grow on soils that are quite saline at depth. This study is a continuation of that research, examining in closer detail the characteristics of naturally saline sites that support boreal forest communities and the response of two boreal forest tree species to soil salinity.

1.2. Plant-salt interactions

Whether naturally present or caused by human actions, salt-affected soils around the world present challenges to the management and conservation of plant communities because of the negative effects of salinity on plant growth. Non-halophytes, plants that are not adapted to saline conditions, suffer in the presence of excess salts in the soil. Salt-induced plant stress is caused by two main mechanisms: water deficit and/or ion excess, as described by Greenway and Munns (1980). Water deficit conditions are created by high concentrations of any ions in the soil which change the osmotic balance between the root and the soil, reducing a plant's ability to take up water and nutrients. Via this mechanism, plant stress is related to the total concentration of solutes, generally measured by electrical conductivity, and not the specific type of salt. Specific salt ions are important for the second mechanism because they have differential effects in causing toxicities or interfering with plant metabolic pathways (Allen et al. 1994). For example, when sodium concentration is high, it can interfere with the uptake of essential nutrients (e.g., calcium, magnesium, or potassium). A high concentration of calcium would be less likely to disrupt plant functions than sodium. Chloride is also often a culprit causing plant stress and has been associated with decreases in shoot nitrate concentrations (Grattan and Grieve 1993). The degree to which water deficit or ion excess is responsible for reduced growth in plants affected by salinity is difficult to determine (Greenway and Munns 1980) and continues to be an area of interest in plant physiology; further insights are now possible because of advances in molecular biology (Sairam et al. 2006).

The majority of research on plant-salt interactions has been on agricultural plants, which typically have a threshold salinity tolerance. At salt concentrations above the threshold, plant growth decreases linearly with increasing salinity (Maas 1986). Water deficit reduces water uptake as well as nutrient uptake in proportion to the concentration of total dissolved salts in the soil. Woody plants can have a salt tolerance response curve different from herbaceous crops because woody plants are more vulnerable to salt-injury by ion toxicity, especially from sodium and chloride; growth of woody plants may not decrease linearly with salinity (Maas 1986). Leaf death from ion accumulation can inhibit woody plant growth at relatively low salinity levels, depending on the effects of specific salts on specific plant species (Maas 1986).

The salt tolerance of a crop species is related to factors besides the amount and type of salts. The availability of essential nutrients, especially nitrogen, can

play a role in crop yield in saline soils. At low or moderate levels of salinity nitrogen can be more limiting to plant growth than salinity; at high levels of salinity, however, nitrogen availability may be irrelevant (Grattan and Grieve 1993). Other nutrients can also interact with salinity to affect plant growth. For example, the ratio of calcium to sodium can be especially important for woody plants (Maas 1986). Because woody perennials live longer than herbaceous crops, there are likely other differences in plant-salinity-nutrient interactions between the two growth forms.

To survive and reproduce in saline soils, non-halophytes can try to avoid salt stress by preventing ion entry through the cell membrane or by pumping ions out of the cell (Allen et al. 1994). When salts do accumulate in plant tissues, non-halophytes often have some ability to store salts in vacuoles, or at least in the less sensitive areas of the plant. For woody plants, the ability to exclude sodium and chloride from foliar tissues is thought to be an important salt tolerance mechanism (Allen et al. 1994). A hypothetical model explaining this mechanism was developed by Munns (1993). Munns proposed that a plant's initial growth response to salinity is due to water-stressed roots sending inhibitory signals to slow plant growth; different genotypes within a species have similarly decreased growth at this stage. Munns described the secondary growth response as a function of how quickly leaves begin to die from salt accumulation; varieties differ in growth response in the second stage either because roots of more salt tolerant plants inhibit salt movement to the shoots, or because cells are more able to adequately separate salts from the cytoplasm in vacuoles. In more salt-sensitive species and genotypes, salt toxicity in foliage happens faster because salts arrive more quickly from roots or are not efficiently compartmentalized in vacuoles (Munns 1993). In long-lived species, the oldest foliage will have the highest salt concentration and be the first to die because – compared to younger foliage – salts would have had more time to arrive through the transpiration stream and accumulate (Munns 1993); this pattern has been observed in *Picea* spp. (Kayama et al. 2003). Munns' model would also predict that long-lived species (i.e. woody plants) will be more sensitive to ion accumulation than herbaceous species because ions accumulate over time – another prediction supported by the literature (Maas 1986, Allen et al. 1994).

Interaction between plants, salinity, and other environmental factors is an active area of research with immediate applications to land management. In this regard, much less work has been done on woody plants than on herbaceous crops, and work on woody boreal forest species has mostly taken place in only the last 20 years. Recent work has focused on boreal forest in the oilsands region of Alberta, where salt tolerance and high productivity traits are desired in species used for revegetation of salt-affected soils.

1.3. Previous research in the boreal

Most research on plant-salinity interactions in the boreal has been done on individual species in short term greenhouse or field trials. Howat (2000) summarizes much of this work. Generally the survival and growth of boreal

species decrease with increasing salinity (McKenzie et al. 1994, Maynard et al. 1997), similarly to non-halophytes around the world, although some species show more resistance to salt than others. Some types of hybrid poplar (e.g., *Populus deltoides* × *Populus balsamifera*), *Cornus stolonifera* Michaux, and *Sheperdia canadensis* (L.) Nutt showed greater resistance to stress associated with application of oilsands composite tailings water than other woody species (Renault et al. 1999). In these short term trials, concentrations of salt ions in the tissues of boreal plants increased with increasing salt concentration in the soil. Species such as *Cornus stolonifera* (Renault et al. 2001) and jack pine (*Pinus banksiana* Lamb.) (Franklin and Zwiazek 2004) appeared to differ in their ability to exclude salt ions from their foliage; this ability may determine which species are more salt-tolerant (Allen et al. 1994).

The type of salt is another important factor influencing plant response; jack pine avoided uptake of Na_2SO_4 better than NaCl (Franklin and Zwiazek 2004); similarly, black spruce (*Picea mariana* [Mill.] B.S.P.) had increased stress when Cl^- was present (Redfield and Zwiazek 2002). White spruce (*Picea glauca* [Moench] Voss) seemed to be more sensitive to Na_2CO_3 than it was to soluble fertilizer salts (e.g. NH_4^+ and NO_3^{2-}; Phillion and Bunting 1983, Maynard et al. 1997) at the same electrical conductivity. Generally, when compared to the effect of other common salts, the combination of sodium and chloride seems to be the most harmful for boreal species (e.g. Nguyen et al. 2006), as well as for plant species around the world (e.g. Martin and Koebner 1995, Kayama et al. 2003).

Another factor affecting the response of boreal forest species to salinity is mycorrhizal associations. Mycorrhizae have been shown to help black spruce, white spruce, and jack pine resist salt ion accumulation (Nguyen et al. 2006). In the field, nearly all boreal forest species form mycorrhizal associations (Allen 1991, Read 1991) and this could have a profound influence on their growth and survival in saline soils, depending on the plant and fungal species.

Several studies have found high variation among individual conifer seedlings in response to salinity stress (Renault et al. 1998). These observations suggest that genotype is another important factor in boreal plant salt tolerance. If there are individuals or populations of boreal species with increased salt tolerance, specific genotype selection could improve reclamation success. Other potential differences in salt tolerance among plant communities, species, and individuals are important for reclamation decisions because of the high investment needed to re-establish plants on disturbed sites. Planting or seeding the wrong suite of species on a site could be a waste of resources and have other undesirable environmental consequences (e.g. soil erosion). Thus, it is important to know which species and genotypes are suitable for what conditions.

The majority of salinity research on tree species of the boreal forest has been on seedlings. Consequently, the long term survival and growth rates of most species growing in salt affected soils are unknown. This study uses naturally saline sites that host well established boreal forest communities to examine the salt tolerance of mature plants, plant community composition of saline sites, and the potential growth rates of trees growing on saline soils. These naturally saline

sites offer the opportunity to understand how salinity affects boreal forest plants in a realistic setting, over a plant's lifetime.

1.4. Objectives

The first objective of this study was to describe the groundwater, soil, and plant community characteristics of naturally saline sites, to understand the salt tolerance limit for boreal forest communities in nature, and to use this information as a model for the reclamation of salt-affected soils. The ability of plants to survive and grow in salt-affected soils will depend on many environmental parameters that could interact with salinity. We quantified soil moisture content, temperature, and nutrient concentrations, and measured groundwater depth and chemistry to understand the combination of conditions that results in successful forest growth on saline soils in the boreal forest.

The second objective was to examine the relationship between soil salinity and the growth of dominant tree species at these sites: aspen (*Populus tremuloides* Michx.) and white spruce. No previous work in the boreal forest has documented the long-term effects of salinity on tree growth; this work will help fill that knowledge gap. Aspen and white spruce are economically the most important tree species in northern Alberta, so understanding their potential growth on saline soils has immediate ramifications for meeting regulatory reclamation requirements on salt-affected soils.

The third objective was to understand the effect of soil salinity on the physiology of the dominant tree species, aspen and white spruce. We explored this aspect by examining the concentrations of salt ions, micronutrients, macronutrients, and the nitrogen and carbon stable isotope ratios in the foliage of aspen and white spruce growing on naturally saline soils. These parameters can give some insight into whether or not salinity is affecting water and nutrient uptake or ion balance in leaves and needles, the tissues these trees depend upon for photosynthesis.

Collectively, this research uses rare saline boreal ecosystems to further our knowledge of the complex relationships and interactions between plant communities and their multidimensional edaphic environment. We address these issues in the context of reclamation in salt-affected soils of the oilsands region, where new information could immediately advance reclamation practices. This work will add to the growing body of knowledge related to oilsands reclamation and assist in the recovery of these heavily disturbed landscapes.

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Chapter 2. Soil and Vegetation Characteristics of Naturally Saline Boreal Forest Stands

2.1. Introduction

In Alberta's boreal forest, the distribution of vegetation across the landscape is primarily determined by water. Over much of the landscape, there is too much water for most trees to grow and a patchwork of sphagnum bogs and stunted black spruce stands dominates. On very coarse textured upland soils that do not retain water, jack pine tends to prevail, forming open forests with lichen dominated understories. The more productive forest stands in the boreal forest occur on mesic sites that have a balanced supply of water and air in the soil; these are the boreal mixedwood sites, dominated by aspen and white spruce.

Even on mesic sites water can be scarce in the summer and drought can contribute to forest dieback or increased susceptibility to pests and disease (Hogg et al. 2002). Hydrological factors like precipitation, evapo-transpiration, soil water holding capacity, topographic position, and water table level all affect how much water is available for plant processes, and what vegetation community develops at a site (Stefan et al. 2007). When another factor that affects plant-water relations – salinity – is introduced to the hydrological system, a completely different plant community could develop on a site. Or, in the worst case scenario, plants may be unable to survive at all. Concerns about plant survival when salinity is present are particularly strong for forest communities because long-lived woody species can be the most sensitive to salinity (Maas 1986). Evidence that typical boreal mixedwood forests can develop when salinity is a part of the hydrological system (Purdy et al. 2005) was surprising, because most research has found salinity to have a major influence on community composition; in shrub, meadow, and wetland vegetation where salts were present, community composition responded foremost to gradients in soil salinity (Lieffers 1984, Burchill and Kenkel 1991, Purdy et al. 2005).

The study of plant-water-salinity relations in the boreal forest is of utmost relevance today because of the impact that oil and gas development has on soil salinity. In the oilsands region of Alberta, a significant portion of the reclaimed landscape will be affected by salinity. Across Alberta, brine is used for drilling operations and can enter the hydrological system during accidental spills or during disposal. The detrimental effects of salinity on plant growth present a formidable reclamation challenge to the oil and gas industry. Any insights into how the boreal forest interacts with salinity and water at naturally saline sites would play a key role in understanding how reclaimed salt-affected landscapes might function.

To meet the challenge of establishing boreal forest communities on salt affected soils, information is needed regarding the level of salinity that trees and understory plants can tolerate. Hydrological factors such as soil moisture, soil nutrients, groundwater chemistry, and water table level could interact with salinity to determine the salinity tolerance, species composition, and community structure

of boreal forests growing on saline soils. These factors can be manipulated to some extent on reclaimed landscapes to create suitable conditions for plant growth. As reclamation proceeds from landscape design, to soil construction, to revegetation, the preparation at each step will depend on our understanding of plant-water-salinity relationships.

Once conditions suitable for plant growth have been created on a reclaimed site, it is essential to know which species would be good candidates for revegetation. Ideally these species would be self-maintaining (TERRE Workshop 1998) and the site would progress normally through succession. When a reclaimed site will be managed for timber production, the potential volume of commercial wood grown on site is another consideration in revegetation decisions. After a disturbance, oil and gas companies are required to create soil conditions that have an equivalent capability for productivity as had the soils that existed before disturbance (Ministry of Sustainable Resource Development 2007, TERRE Workshop 1998). Regulations also require that pre-disturbance biodiversity levels are established on reclaimed sites using native species (TERRE Workshop 1998). Other goals for reclaimed sites include establishing wildlife habitat and traditional aboriginal plants. These regulations and goals also apply to salt-affected sites, and there is a dearth of knowledge about how salinity interacts with other environmental factors to affect the establishment and growth of a variety of native plant species.

The objective of this study was to use naturally saline forest stands in northern Alberta as models for the successful reclamation of salt-affected soil. One could summarize this investigation of plant-water-salinity interactions in the reclamation context under two broad questions about forested saline soils: *i*) What are suitable conditions for plant growth? and *ii*) What are suitable plants? We used an observational approach to answer these questions, sampling the soil, groundwater, and vegetation along salinity gradients to describe saline forest ecosystems that work.

2.2. Methods

2.2.1. Site selection

We located seven naturally saline forested sites in northern Alberta each of which included a gradient of soil salinity. Three sites were located in the Northern Mixedwood natural region: Benchmark, Salt Pan Lake, and Salt Plains (Table 2.1, Figure 2.1). Three sites were located in the Central Mixedwood natural region: Clearwater, Saline Lake, and Zama Marsh. Child Lake was the only site located in the Dry Mixedwood natural region (Figure 2.1, Natural Regions Committee 2006). To simplify the interpretation of forestry data, we chose stands of distinct forest types including white spruce dominated (Benchmark, Clearwater, and Salt Plains), aspen dominated (Child Lake, Salt Pan Lake, and Zama Marsh), and a mixed assemblage of tree species (Saline Lake).

2.2.2. Plot set-up along the salinity gradient

Each naturally saline forested site was adjacent to a saline lake, wetland, or meadow and had a distinct boundary between forest vegetation and grass or shrub dominated vegetation (Figure 2.2). At every site, we wanted to establish plots at three locations along a gradient of salinity, which was anticipated to exist from the saline unforested area into the forest interior, i.e. further away from the saline influence (Figure 2.2). We used an instrument called an EM-38 (Geonics Ltd., Mississauga, Ont., Canada) to survey along the salinity gradient and identify appropriate locations for 100 m^2 sampling plots at high, medium, and low salinity levels (Figure 2.2). We also used the EM-38 to ensure that the salinity was spatially consistent within the 100 m^2 area of each plot. The EM-38 uses an electromagnetic inductance technique to read the conductance of the soil beneath it. When used in the vertical position, as in this study, the reading is influenced by exchangeable ions, soluble ions, and soil moisture and temperature from 0 to 1.5 m in depth (McKenzie et al. 1989). When salinity increases with depth, as it did at our study sites, the deepest portions of the soil have the strongest influence on the EM-38 reading because they have the highest conductivity (McNeill 1980). Therefore, our salinity surveying with the EM-38 predominantly measured the conductivity of the soil between 1 and 1.5 m (the parent geological material [PGM]) and the high, medium, and low salinity plots were based on relative differences in the salinity of the PGM within a site. At each site the high salinity plot was located adjacent to the forest edge (the limit of salinity tolerance for trees at each site) and the low salinity plot was located where the least saline soils were found at the site. Salinity varied with depth in the soil profile at each site and the levels of salinity varied among sites. As such the 'high', 'medium', and 'low' levels of salinity were only relative to each other within a site and not between sites. We hereafter refer to the three locations along the salinity gradient at each site simply as 'high', 'medium', and 'low' because there was no single quantitative measure of salinity in any plot. We did measure electrical conductivity throughout the soil profile in each plot (see below).

From EM-38 surveying of the sites, we discovered that the salinity often decreased very rapidly from forest edge to forest interior. To ensure that each plot had consistent salinity we used 5×20 m plots with the long edge parallel to the forest edge (Figure 2.2) except at Saline Lake where the salinity decreased so rapidly that it was necessary to use 3×33.3 m plots parallel to the forest edge.

2.2.3. Soil sampling and analysis

Soils were sampled in 2005 or 2006. In each plot we dug three soil pits: one central soil pit, and pits between the center and each plot end (Figure 2.2). The soil in each plot was classified according to the Canadian System of Soil Classification (Soil Classification Working Group 1998); the Clearwater soils were also described with horizon letters recommended Fox et al. (1987) for Folisols. We sampled the soil by horizon and bulked the corresponding soil samples from each pit into one sample per horizon for each plot. By bulking soil samples in each plot we lost information about within plot variability in soil properties, so moderate differences in soil properties among plots will be

discussed as trends only. We also used a slide hammer to take two bulk density samples from horizons greater than 7 cm in thickness. To compare the salinity of the topsoil in the sample plots, where trees were growing, to that in the adjacent area where there were no trees growing, we collected three additional samples from outside the forest at each site and bulked them. These 0-20 cm deep samples were collected 2-5 meters outside of the forest edge adjacent to the high salinity sampling locations.

In the laboratory, all samples were air dried and ground to pass through a 2 mm sieve. We measured electrical conductivity (EC) with an Accumet® conductivity meter (Fisher Scientific, Ottawa, Ont., Canada) on all samples in a saturation paste extract (Sparks 1996) without adding $(NaPO_3)_6$. Soluble Na^+, K^+, Ca^{2+}, and Mg^{2+} concentrations were measured with a SpectrAA 880 (Varian Inc., Mississauga, Ont., Canada) Atomic Absorption Spectrometer on the saturation extracts and used to calculate the sodium absorption ratio (SAR = $[Na^+]/\sqrt{([Ca^{2+}]+[Mg^{2+}])}$). Soluble Cl^- and SO_4^{2-} concentrations were also measured on the saturation extracts by ion chromatography with a DX600 (Dionex Corp., Sunnydale, CA, USA). In order to make comparisons among sites that had different horizons we calculated weighted EC, SAR, and ion concentrations by depth for three depths: topsoil (0-20 cm), upper subsoil (20-50 cm) and lower subsoil (50-100 cm). The pH of every sample was measured with an amplified pH electrode in the supernatant of 1:2 soil to water mixtures for mineral soils and 1:5 mixtures for organic soils (Kalra and Maynard 1991).

The Bouyoucos hydrometer method (Kalra and Maynard 1991) was used to measure particle size on all mineral soil samples with appropriate pre-treatments for organic matter, soluble salts, and carbonates. Available water holding capacity (AWHC) was calculated for each plot using the particle size composition and horizon depths according to the Land Capability Classification System (LCCS; Leskiw 2006), but the soil moisture regime of Saline Lake as calculated from the LCCS did not fit our field measurements and observations so it was adjusted upwards. The soil nutrient regime of each plot was also estimated with the LCCS (Leskiw 2006).

2.2.3.1. Soil nutrients

Total carbon and nitrogen, mineralizable nitrogen, cation exchange capacity, and exchangeable Ca^{2+}, Mg^{2+}, Na^+, and K^+ were determined only in the forest floor samples and the soil horizons within 20 cm of the forest floor. Samples were finely ground with an electronic ball grinder and combusted using the Dumas method (Carter 1993) with a Carlo Erba (*now* CE Elantech Inc., Lakewood, NJ, USA) NA1500 Elemental Analyzer to determine weight percent total carbon and nitrogen. Inorganic carbon was eliminated from samples with carbonates (with HCl) to ensure that total carbon values were organic carbon only. Mineralizable nitrogen was measured with a 2-week anaerobic incubation procedure at 30 °C using 10 g mineral soil or 2.5 g organic soil and 25 mL of water in 20×150 mm stoppered test tubes. To prevent stoppers from popping off during incubation, 5 mL of air was removed from tubes (with a syringe) and discarded before incubation. The total NH_4-N released after incubation was

considered to be an index of potential mineralizable nitrogen (Powers 1980). Released NH_4-N was extracted from samples with 2M KCl (Powers 1980). For soil samples without carbonates (pH < 7.0) exchangeable and soluble cations were extracted with 1M NH_4Acetate at pH 7.0 and determined with the SpectrAA 880 Atomic Absorption Spectrometer. The soluble cations, as determined from the saturation extract, were subtracted from the total exchangeable and soluble cations to calculate exchangeable Ca^{2+}, Mg^{2+}, Na^+, and K^+ as recommended by the US Salinity Laboratory Staff (Richards 1954). Total cation exchange capacity (CEC) was measured in all samples with an NH_4Acetate extraction and displacement of NH_4^+ with Na^+ (McKeague 1978). Exchangeable Ca^{2+} and Mg^{2+} in soil samples with carbonates (and other samples where exch. Ca^{2+} + Mg^{2+} + Na^+ + K^+> total CEC) were estimated with the Gapon Exchange Equation (Richards 1954):

$$\text{Exchangeable sodium ratio (ESR)} = K_G \times SAR + b$$

or

$$\text{exch. } Na^+ / (\text{exch. } Ca^{2+} + Mg^{2+} + K^+) = K_G \times SAR + b$$

where K_G is the Gapon exchange constant and b is the intercept; both K_G and b vary among different soil types (Endo et al. 2002) so they were estimated for these sites using regression equations derived from the carbonate free soil samples. The equation ESR = 0.027×SAR - 0.026 (R^2 = 0.86, n = 5) was used for the Benchmark soils and the equation ESR = 0.0072×SAR + 0.019 (R^2 = 0.81, n = 13) was used for all other sites. The NH_4Acetate extraction method did not give repeatable results for organic soils so CEC data were not used for those soils. NH_4-N concentration for mineralizable N and total CEC extractions was determined by autoanalyzer colorimetry with an AutoAnalyzer II (Technicon Instruments Corp., Tarrytown, NY, USA). To convert all of these data into per hectare values, the data on horizon thickness and bulk density values were used. Bulk density and air dry soil moisture contents were calculated by drying the samples at 105 ˚C for 24 hours. All soil nutrients are given on a per dry weight basis.

2.2.3.2. Soil and groundwater monitoring

We used environmental monitoring equipment to measure soil temperature, soil volumetric water content (θ; here used synomously with soil moisture content), and the water table level in each plot throughout the growing season of 2006. Soil temperature was monitored with HOBO H8 (Onset Computer Corporation, Bourne, MA, USA) sensors. HOBO H8 sensors were installed centrally in each plot 10 cm below the forest floor (Figure 2.2); they were buried in May and removed at the end of October, 2006. EasyAg 50 (Sentek Sensor Technologies, Stepney, SA, Australia) soil moisture probes were used to monitor θ at 10, 20, 30 and 50 cm below the forest floor in one central location per plot (Figure 2.2). Soil volumetric water content was manually measured twice during the growing season and used to calibrate the EasyAg probes; the first measurements were taken on soil samples collected midseason from within 10 m

of the probes at the proper depth, the second, more accurate, measurements were taken from within 5 cm of each probe sensor when the probes were removed at the end of the growing season. The volumetric water content at field capacity and wilting point were estimated for topsoils using particle size composition equations based on soil texture–soil water relationships; Saxton et al. 1986, Pedosphere.com 2004). Odyssey capacitance water table level probes (Dataflow Systems Pty. Ltd., Christchurch, New Zealand) were used to monitor the ground water level in each plot in 2.0 m deep wells (Figure 2.2). Groundwater samples were collected from wet wells in midsummer 2006 and analyzed for pH, EC, and concentrations of Na^+, K^+, Ca^{2+}, Mg^{2+}, NH_4^+, Cl^-, SO_4^{2-}, and HCO_3^{2-}; ions were determined with inductively coupled plasma with optical emission spectroscopy and ion chromatography at the Syncrude Canada Laboratory in Edmonton, Alberta. Correlations between chemical parameters in the groundwater and the lower subsoil solution were examined using SAS Version 9.1 (SAS Institute Inc., Cary, NC, USA); Spearman correlation coefficients were reported because of frequent outliers in the data. We were unable to install monitoring equipment at the Benchmark site due to its remote location, but we were able to drill wells, measure the water table level and collect groundwater samples in midsummer 2006. Aerial photos of the sites were examined for changes over time in the water level and surface salt crusts at adjacent saline wetlands.

2.2.4. Vegetation sampling and analysis

In every plot we identified to species and counted every live tree and every snag with a diameter at breast height (1.3 m; DBH) over 5 cm. For each live stem, DBH was recorded and height was measured with a Haglöf Vertex III Ultrasonic Hypsometer. The total volume and merchantable volume of each tree were calculated using published equations for Alberta (Huang 1994); volumes of individual trees were summed for total plot volume. Merchantable volume was the total tree volume minus the volume of the tree tip (portion of tree top with an inside bark diameter of < 2.0 cm) and the volume of the stump (portion of tree base below 0.3 m in height). If less than 10 live trees were counted in a plot, we extended the plot by 5 meters on each end to get a 150 m^2 plot that contained at least 10 live trees.

The percent cover of every understory vascular plant species (including tree species with a DBH < 5 cm) was measured as the cover over the entire plot in cover classes of < 1, 1-3, 4-10, 11-25, 26-50, 51-75 and > 75 percent. Taxonomy was according to Packer (1983). Plants were identified to species except for the *Carex*, *Salix*, and *Sonchus* species. To examine patterns of variation in plant community composition among plots within and between sites we used nonmetric multidimensional scaling ordination (PC-ORD Version 4.5, MJM Software Design, Glenedon Beach, OR, USA; McCune and Mefford 1997). The median value of the cover class per species per plot was used as the data set into the ordination, these data were then log transformed and the Bray-Curtis distance was used as the similarity measure; an automated procedure supplied the random starting configuration (McCune et al. 2002). Plant community data and soil data

were also used to classify plots according to ecosite (Beckingham and Archibald 1996).

2.3. Results

2.3.1. Soil characteristics

2.3.1.1. Classification

We found forest stands growing on a wide range of naturally saline soils over six soil orders: Regosolic, Brunisolic, Luvisolic, Gleysolic, Solonetzic, and Organic (Figure 2.3). Moving from the high salinity plot near the forest edge to the low salinity plot in the forest interior, soil characteristics generally remained quite similar, but some sites did seem to have slightly different soil genesis histories along the gradient. At Clearwater, Salt Plains, and Salt Pan Lake, the soil subgroup remained the same along the salinity gradient. At Benchmark, Child Lake, Zama Marsh and Saline Lake soil characteristics changed enough along the salinity gradient for the soils to be considered different subgroups. At Benchmark, the low salinity soil was a Solod compared to the Solodized Solonetzes in the medium and high salinity soils. This low salinity soil was much further from the water table than the medium and high salinity soils and presumably had been desalinized (due to the leaching of salts by precipitation) for the longest time (Magistad 1945). The low salinity soil had progressed the furthest in soil genesis; the upper portion of the solonetzic B horizon had eluviated and broken-down into Ae and AB horizons (Figure 2.3). Along the salinity gradient at Child Lake, the soils decreased in organic matter content in the A horizon and in salinity influence in the B horizon (Figure 2.3, Appendix D). Zama Marsh soils were all solonetzic, but the soil in the low salinity plot had more evidence of saturated conditions than in the other plots, so it was classified as a Solonetzic Luvic Gleysol. The opposite occurred at Saline Lake where the high salinity soil was more affected by a high water table and classified as a Gleyed Cumulic Regosol.

2.3.1.2. Electrical conductivity

In all the naturally saline forested soils we sampled, the EC of the topsoil was at or below 4.1 dS/m, with a range from 0.2 to 4.1 dS/m. The EC of the topsoil 2-5 m outside of the forest edge was always above 4.1 dS/m (Figure 2.4). The EC of the upper subsoil ranged from 0.2 to 9.4 dS/m, and the EC of the lower subsoil ranged from 1.7 to 23dS/m.

The electrical conductivity in the top meter of soil decreased at these sites from forest edge to forest interior. This pattern was evident at every site and the largest change in EC was found in the lower subsoil, followed by the upper subsoil (Figure 2.5). The highest EC's measured were almost always in the deepest soil closest to the forest edge (high salinity plot), but there were large differences between sites in the highest EC measurement. Salt Pan Lake was the least saline site with a high EC of 4 dS/m at 100 to 130 cm in depth. Saline Lake was the second least saline site with a high EC of 5 dS/m from 80 to 100 cm deep. The highest EC measurements for Zama Marsh, Benchmark, and Child Lake were

9, 10, and 15 dS/m, respectively. Clearwater (highest EC = 19 dS/m) and Salt Plains (highest EC = 30 dS/m) were the most saline sites.

Generally the EC results confirmed the 'high', 'medium' and 'low' salinity designations determined with the EM-38. At most sites the highest EC was found in the high salinity plot and the lowest EC in the low salinity plot, with the medium salinity plot intermediate in EC. However, at Zama Marsh, EC values in the lower and upper subsoil of the medium salinity plot were very similar to the high salinity plot, and the medium salinity plot actually had slightly higher EC in the topsoil, at least when we measured in August, 2005.

2.3.1.3. Sodium absorption ratio

All seven sites in this study were dominated by sodium salts in the groundwater and soil. Along the salinity gradient, the sodium absorption ratio generally followed the same trend as the EC, with the highest SAR values in the lower subsoil of the high salinity soils, and the lowest SAR values in the topsoil of the low salinity soils (Figure 2.6). Zama Marsh was the only site that varied from this trend with a higher SAR in the upper subsoil than the lower subsoil, which was caused by reduced levels of soluble Ca^{2+} and Mg^{2+} in the upper subsoil.

All of the sites we sampled had lower subsoils with SAR > 12, at least in the high salinity plots. Benchmark, Clearwater, Salt Plains, Child Lake, and Zama Marsh also had sodic (SAR ≥ 13) upper subsoils, and Clearwater, Salt Plains, and Zama Marsh had sodic topsoils.

2.3.1.4. Soil reaction

The pH of the lower subsoil was above 7.0 at every site, which is common for soils in Alberta. Benchmark, Salt Plains, Salt Pan Lake and Zama Marsh had soils with strongly alkaline (pH ≥ 8.5) conditions (Figure 2.3). The two sites with Regosolic soils, Salt Plains and Saline Lake, had alkaline conditions throughout the topsoil (Figure 2.3). Salt Plains was the most alkaline site with pH values from 6.9 to 8.1 in the topsoil, and from 9.0 to 9.4 in the upper subsoil. The topsoil pH at Saline Lake was between 7.2 and 7.4. The forest floor and uppermost portions of the soil profile at the other five sites had pH values in the acid range, similar to most non-saline forest soils on mesic sites in this region.

2.3.1.5. Soil moisture content

Soil moisture content in the topsoil (10 cm measurement) tended to remain at or above the estimated field capacity at the white spruce sites, whereas it tended to fluctuate between field capacity and the permanent wilting point at the aspen and mixedwood sites (Table 2.2). There were no consistent trends in θ along the salinity gradients.

At the white spruce sites the topsoil had more than 25% soil water content throughout the growing season and mean differences in θ within and among sites were not more than 16% (Table 2.2). Benchmark had 12-16% more soil water in the high and medium salinity plots than the low salinity plot the one time we sampled; plots within Clearwater and Salt Plains had mean θ within 8% of each

other. The upper subsoil θ was generally between 40 and 60% at Clearwater, between 30 and 35% at Salt Plains (Appendix G), and between 41 and 47% at Benchmark.

Among the aspen sites, Salt Pan Lake had the lowest mean θ (≤ 16%). Soil moisture content in the medium and low salinity plots fluctuated during the season from the wilting point to above field capacity, but θ in the high salinity plot remained near field capacity. Child Lake had the second lowest mean θ: 19 to 21% at 10 cm (Table 2.2). Minimum and maximum θ were close to wilting point and field capacity estimations, respectively, for all plots. Although θ was similar among plots at 10 cm, θ in the upper subsoil tended to increase with decreasing salinity (Appendix G). At Zama Marsh, mean topsoil θ tended to increase with decreasing salinity: from 35 to 46% (Table 2.2), but upper subsoil θ was similar among plots at close to 40 % (Appendix G). Maximum values for θ tended to be lowest in the high salinity plot at Zama Marsh – below estimated field capacity. At Saline Lake, upper subsoil θ decreased with decreasing salinity (Appendix G) and the low salinity plot topsoil also had the lowest θ with 16 to 39 % soil water content (Table 2.2). This was the only plot at Saline Lake with a minimum θ at the estimated wilting point.

2.3.1.6. Soil nutrients

Every site had a medium-rich or rich nutrient regime, except the low salinity plot at Child Lake which had a medium (nearly medium-rich) nutrient regime, according to the LCCS (Table 2.1; Leskiw 2006). Saline Lake was probably the richest site because of the buried organic layers below 20 cm in depth (Figure 2.3). There seemed to be some differences in soil nutrient concentrations along the salinity gradient at the white spruce sites, but at Benchmark and Clearwater some nutrient concentrations increased with salinity while others decreased (Table 2.3). Only the Salt Plains site had a more consistent trend; total C and N, mineralizable N, and exchangeable Ca^{2+} and Mg^{2+} seemed to increase from the high salinity to the low salinity plot. This result was due to the increase in the depth of the forest floor with decreasing salinity at Salt Plains (Figure 2.3); by horizon, nutrient concentrations were similar among plots (Appendix D).

The aspen and mixedwood sites had more obvious trends in soil nutrient concentrations along the salinity gradient. Every site had a greater total C and mineralizable N concentrations in the high salinity plot compared to the other plots (Table 2.3). Child Lake, Zama Marsh, and Saline Lake also had the highest total N and exchangeable Ca^{2+} and Mg^{2+} concentrations in the high salinity plot. The increased nutrients near the forest edge at Child Lake and Zama were mostly found in A horizons enriched in soil organic matter. These soils were likely developed by a grassland or meadow plant community that existed before the encroachment of forest vegetation. The Salt Plains and Salt Pan Lake sites also had soils with A horizons enriched in soil organic matter, suggesting that the soils developed under the influence of a non-forest plant community for hundreds or thousands of years before forest vegetation was established.

2.3.1.7. Soil temperature

The soil temperature at these sites scattered around northern Alberta seemed to follow the same peaks and troughs throughout the growing season of 2006 (Figure 2.7). At most of the sites there was very little difference in soil temperature along the salinity gradient. The Salt Plains was the exception, with soil temperature decreasing from the high to low salinity plots. The depth of the forest floor increased along the salinity gradient at this site and seemed to insulate the soil, thereby creating cooler summer temperatures. In 2005 we found frozen soils at 50 cm depth in the low salinity plot. Saline Lake had slight differences in soil temperature between plots with larger fluctuations in temperature in the low salinity plot. This plot was furthest from the lake so soil temperatures were probably less affected by the temperature moderating influence of a large body of water.

2.3.1.8. Water table level

The water table was within 2 m of the mineral soil surface at every site sometime during the growing season of 2006 (Table 2.2). The medium and low salinity plots at Benchmark, and all plots at Salt Plains and Salt Pan Lake, tended to have deeper water tables with mean depths of over 1 m (Table 2.2). The high salinity plot at Benchmark and Saline Lake, and all plots at Clearwater, Child Lake, and Zama Marsh had shallower water tables, often at or above 50 cm for part of the growing season (Table 2.2). Among plots within a site, there was little water table level change at Clearwater and Salt Plains. At Salt Pan Lake and Saline Lake, we encountered bedrock before the water table in the medium and low salinity plots, so it is difficult to compare within site water tables. The water table level decreased with increasing elevation and decreasing salinity at Benchmark (Table 2.2 Appendix F). The two sites with water tables that came right up to the mineral soil surface, Child Lake and Zama Marsh, also tended to have the largest fluctuations in water table level (Table 2.2). We surmise that during the first half of the summer (May-July) at these sites, water perched above the relatively impermeable B horizons, causing the gleyed and mottled conditions found in the topsoil at Child Lake and Zama Marsh (Figure 2.3). The high salinity plot at Child Lake was at a higher elevation that the other plots, had a deeper water table, and did not have gleying and mottling in the topsoil (Table 2.2, Figure 2.3, Appendix F). Fluctuations in water levels at these sites seem to occur from year to year as well as seasonally. In 2006 we could barely access Zama Marsh with a quad, yet in 2004 it was accessed with a truck. Past aerial photos of Zama Marsh clearly illustrate remarkable changes in water levels and surface salt crusts over time (Figure 2.8).

2.3.1.9. Groundwater chemistry

Groundwater anion chemistry of every site except Zama Marsh was dominated by chloride (Figure 2.9). Significant correlations existed between some of the major ions and other chemical measurements in the soil solution and groundwater (Table 2.4), suggesting that there was a direct influence of the groundwater on soil chemistry. Chloride and sulfate in the groundwater were

more closely correlated to chloride and sulfate in the soil solution than any cations were correlated between the groundwater and soil solution, suggesting that individual cations in the soil solution were less directly affected by the groundwater than individual anions.

2.3.2. Vegetation characteristics

Variation in composition of the understory community among plots within a site was minimal. Slight changes in species dominance along the salinity gradient were probably related to increased light availability at the forest edge compared to the forest interior. The aspen dominated sites tended to have more *Amelanchier alnifolia* Medic. at the forest edge than in the forest interior. Feather mosses tended to become more dominant in white spruce stands as we moved further from the forest edge (Table 2.1). Overstory composition changed along the salinity gradient at Clearwater where balsam fir (*Abies balsamea* [L.] Mill.) became more common further from the forest edge, and at Saline Lake where balsam poplar (*Populus balsamifera*, L.) decreased in abundance further from the forest edge. At Child Lake, Salt Pan Lake, and Zama Marsh the size and number of aspen stems seemed to change along the salinity gradient and with distance from the forest edge, with higher numbers of smaller stems at the forest edge.

2.3.2.1. Overstory characteristics

We found aspen, white spruce, balsam poplar, balsam fir, and paper birch (*Betula papyrifera*, Marsh.) growing on saline soils (Table 2.5). Three sites were dominated by aspen, three were dominated by spruce, and one site had a mix of aspen, balsam poplar, white spruce, and paper birch. The trees at the aspen sites were about 60 years old (except for a young stand at the forest edge at Child Lake), and where white spruce was present, it was beginning to reach the canopy. The canopies were relatively homogeneous with more canopy gaps at Zama Marsh. The white spruce sites generally had much older trees (> 100 years) and a more heterogeneous canopy. Only a few small aspen stems were found at these sites. Clearwater seemed to be at a later stage of succession than the other sites with balsam fir starting to dominate in gaps between white spruce trees. Saline Lake was an unusual site with a mix of species and tree ages and many canopy gaps. This site's position between the Athabasca River and Saline Lake may have prevented it from burning for hundreds of years.

The total volume of wood found in 50+ year old stands at all of the study sites varied from 103 to 480 m^3/ha and merchantable volume ranged from 62 to 343 m^3/ha. Many plots had a total volume between 230 and 400 m^3/ha. The number of stems per hectare in each plot ranged from 667 to 4300, with most being between 1000 and 2700 (Table 2.6). The small size of our plots (0.01 ha) likely contributed to the high variability in forest volumes and prevents us from drawing strong conclusions about the productivity of saline soils based on forest volume data alone (but see Chapters 3 and 4).

2.3.2.2. Understory plant community

The understory vascular plants found on these sites were typical of aspen, white spruce, and mixedwood stands in Alberta's boreal forest. A total of 89 species were found, with an average of 35 species per site and 24 species per plot. The most commonly occurring (≥ 50% frequency) species in the aspen and mixedwood sites were *Achillea millefolium* L., *Amelanchier alnifolia*, *Aster ciliolatus* Lindl., *Calamagrostis canadensis* (Michx.) Beauv., *Cornus canadensis* L., *Elymus innovatus* Beal, *Epilobium angustifolium* L., *Fragaria virginiana* Duchesne, *Galium boreale* L., *Hieracium umbellatum* L., *Lathyrus ochroleucus* Hook., *Linnaea borealis* L., *Lonicera involucrata* (Richards.) Banks, *Maianthemum canadense* Desf., *Picea glauca*, *Pyrola asarifolia* Michx., *Rosa acicularis* Lindl., *Rubus pubescens* Raf., *Salix* sp., *Sheperdia canadensis* (L.) Nutt., *Symphoricarpos albus* (L.) Blake, *Viburnum edule* (Michx.) Raf., and *Vicia americana* Muhl.. The most commonly occurring (≥ 50% frequency) species in the white spruce sites were *Cornus canadensis*, *Elymus innovatus*, *Epilobium angustifolium*, *Galium boreale*, *Geocaulon lividum* (Richards.) Fern., *Hedysarum alpinum* L., *Linnaea borealis*, *Orthilia secunda* (L.) House, *Populus tremuloides*, *Rosa acicularis*, *Rubus pubescens*, *Salix* sp., and *Vaccium vitis-idaea* L. (Appendix A).

The understory species composition at these sites seemed to be most strongly related to the dominant overstory species and to differences between sites, rather than showing an influence of the salinity gradient at each site (Figure 2.10). Plots from the same site tended to group together in ordination space and white spruce dominated plots separated from aspen and mixedwood dominated plots (Figure 2.10). There was no evidence that the level of salinity was related to understory plant community composition.

2.4. Discussion

2.4.1. Salt tolerance of boreal forest species

Our results clearly demonstrate that healthy and productive boreal forest stands can establish on saline soils with a variety of characteristics. Saline brunisols with fine textured soil underneath coarse textured soil can support tree growth, as can saline regosols with alkalinity in the topsoil. Likewise, saline luvisols and saline organic soils were shown to support tree growth. Although solonetzic soils are usually considered grassland soils, they do form in these rare saline sites in the boreal forest, and they certainly support tree growth. The critical factor in determining whether aspen or white spruce can establish on saline soils seems to be the depth at which 'high' salinity is reached, rather than the overall salinity. At all of these naturally saline sites the salinity increased with depth; the lower subsoil electrical conductivity could be as high as 23 dS/m, but the electrical conductivity of the topsoil was at or below 4 dS/m. Additionally, when we sampled the topsoil just outside of where trees had established, the electrical conductivity was always above 4 dS/m. The results strongly confirm the

previously held principle that 4 dS/m is a critical limit for the establishment of forest vegetation.

An electrical conductivity of 4 dS/m has long been considered an important tolerance limit for the growth of most plants; in early salinity research the US Salinity Laboratory identified 4 dS/m as the limit restricting the yield of many crops (Richards 1954). Previous research at naturally saline sites in the boreal forest also concluded that 4 dS/m in the topsoil seemed to be the limit for forest growth (Purdy et al. 2005).

Reduced growth and survival of plants at this salinity level could be caused by water deficit due to decreased soil water potential, or excess ion accumulation in plant tissues (Kramer 1983). We know that salinity decreases the osmotic potential of the saturated soil solution (Campbell et al. 1948) and that plants can absorb water when their internal osmotic potential is lower than the soil water potential, which is affected by osmotic and matric potential (Brooks 1997). Matric potential decreases as soil dries (Brooks 1997) and in saline soils osmotic potential decreases because the salt concentrations in the remaining soil water will increase (Marschner 1986). This could reduce water potential to below the wilting point. In the boreal forest, where water can be limiting to plant growth (Yarie et al. 1990), plants that already experience water stress, will have even more difficulty in absorbing water if osmotic potential is reduced by increasing salt concentrations. The influence of salinity on soil water potential seems a straightforward explanation for why 4 dS/m becomes limiting for plant growth.

Aspen and white spruce are both capable of appreciable osmotic adjustment (Kozlowski and Pallardy 2002) and may be more susceptible to ion excess rather than water deficit in saline soils. In this situation, the harmful effects of within-plant salt accumulation may act as the direct limit to healthy growth, rather than the harmful effects of water deficit (Kramer 1983). Regardless of whether water deficit, ion excess, or a combination of the two causes the most stress for boreal forest vegetation, a topsoil electrical conductivity of 4 dS/m seems to be an important limit for salinity tolerance, and a valid indicator of where forests can and cannot establish.

One surprising result from our research was that the forest floor plus a mere 20 cm of soil with EC less than 4 dS/m, seems to be enough to support typical boreal forest species in the understory and the overstory. Another surprising result is that these species can establish where the upper subsoil SAR is above 12 and the pH is above 9.0; these were previously also considered unsuitable conditions for revegetation in the boreal forest (Howat 2000, Macyk et al. 2004). At pH > 9.0, root cells are usually damaged and some nutrient ions, especially PO_4^{3-}, Fe and Mn, have limited availability (Larcher 1980). In sodic soils, high levels of Na^+ in relation to Ca^{2+} and poor soil physical properties are known to limit plant growth (Marschner 1986). High pH and high sodium often occur together in saline soils; sodium is hydrolyzed to form NaOH and then reacts with CO_2 to form Na_2CO_3; these two soluble salts both raise pH (Magistad 1945) and were most likely present in the soils of this study with pH > 9.0. Despite high pH and sodium in these soils, forest growth persisted. Boreal forest communities

do not require a full meter, or even half a meter, of soil free of excess sodium salts in order to establish.

2.4.2. Soil moisture at saline sites

As discussed above, it is matric potential and osmotic potential that will determine the soil water potential in saline soils, and both are affected by θ. Low soil moisture availability in itself can cause severe plant water stress when matric potentials are near the wilting point (Kramer 1983), and salinity can increase that water stress. High salinity and low θ could be a deadly combination for non-halophytes, causing water potential to frequently dip below the wilting point. We did not find that combination on our sites.

We found that where salt concentrations were high, θ tended to be high as well. At Salt Plains, the most saline site, θ was at or above the estimated field capacity for the whole growing season. At Clearwater, the second most saline site, θ almost always remained above 40%. Soil water content at Benchmark was also above the estimated field capacity, and was highest where salinity was at a medium or high level. In the more saline aspen and mixedwood plots where topsoil moisture fluctuated and was not available all season long, upper subsoil moisture remained available. For the plots that had lower θ in the upper subsoil (the low salinity plot at Saline Lake and the medium and low salinity plots at Salt Pan Lake) the upper subsoil salinity was below 1 dS/m. These results suggest that boreal forests do not develop where salinity is high and soil water content is low.

It is difficult to determine the worst combination of salinity and soil moisture on which boreal forests can still establish because we did not directly measure water potential in this study. By examining changes in θ along the salinity gradient we can only guess at possible interactions between the two factors. At Benchmark and Saline Lake, θ tended to increase with salinity so higher matric potentials may have compensated for lower osmotic potentials along the salinity gradient. At Salt Pan Lake, the fine textured saline parent material was closest to the surface in the high salinity plot. This material had the highest θ and probably helped this topsoil remain at or above field capacity all season, possibly compensating for the salinity of the material. Compensatory interactions between moisture and salinity were unlikely at Clearwater and Salt Plains because θ was consistent among plots. Child Lake and Zama Marsh were the only sites where θ may have decreased where salinity increased; this trend was either in the topsoil (Zama Marsh) or the upper subsoil (Child Lake). It is possible that the high salinity soil water potential at these two sites was dually reduced by lower osmotic potential and lower matric potential compared to the medium and low salinity plots. Forest stands on those soils may be the most vulnerable to drought or to the generally drier conditions expected with climate change in Alberta (Hogg 1994).

2.4.3. Soil nutrients in saline sites

Other research has found that improved soil nutrients can help plants survive in saline and sodic conditions. Higher levels of plant available soil nutrients can partially compensate for increased salinity in some cases. For

example, nitrogen addition usually increases plant growth even in saline soils (Grattan and Grieve 1993). Furthermore, at these saline sites it is reasonable to suspect that if soil moisture and nutrient availability were high enough in the topsoil, then forest plants could avoid rooting in the subsoil where the salinity was less tolerable. We found some indications of nutrients compensating for salinity. For example, at Saline Lake, which had the richest soil, the forest in the high salinity plot had more than twice the volume of wood compared to most other high salinity plots. Although at Child Lake and Zama Marsh the nutrient regime was rich in every plot, the high salinity soils had considerably more total organic carbon and nitrogen concentrations than the lower salinity soils, which could have been a factor facilitating forest establishment on the higher salinity soils even though soil water content tended to be lower.

Soil organic matter can improve both water holding capacity and nutrient availability. This valuable soil component is also known to help compensate for high sodicity (Richards 1954); multiple experiments have shown the beneficial effects of supplying manure to sodic agricultural soils on soil aggregation and plant productivity (Bower et al. 1951, Lüken 1962, Barzegar et al. 1997). It may be more than coincidence that the two sites where forest had established on sodic topsoil had high amounts of organic matter. At a soil SAR of > 13, the exchangeable sodium percent is > 15, and clay particles can disperse if EC < 4 dS/m, leading to degradation of soil physical properties: aggregation, permeability, hydraulic conductivity, and bulk density (Richards 1954). The high salinity topsoils at Clearwater and Salt Plains had SARs of 18, and 16, respectively, and seemingly normal physical properties. The soils were organic at Clearwater and the topsoil had 7.4 % organic carbon at Salt Plains; this organic matter could have prevented soil degradation by feeding soil aggregating microbes, increasing cation exchange, and/or decreasing bulk density (Richards 1954). Soil organic matter content is probably an important factor in allowing forest establishment on sodic soils, especially on sodic topsoils with EC < 4 dS/m.

Soil temperature can be a factor affecting the availability of nutrients, especially of nitrogen, because nitrogen mineralization decreases with temperature (Krause 1991). The largest differences in soil temperature at our study sites were at Salt Plains and seemed to be related to the depth of the forest floor. Floodplain successional studies in interior Alaska also found that thick layers of forest floor organic matter insulated and cooled the mineral soil in late successional forests (Viereck et al. 1993). Clearwater also had a thick forest floor in every plot, but did not have cold soil temperatures; groundwater was continually seeping underground at Clearwater and probably helped warm the soil from the bottom up. Forest productivity on saline soils, like non-saline soils, could be depressed by cold soil temperatures, but this would probably only come into effect after the many decades required to develop a thick forest floor.

2.4.4. Groundwater-soil interactions

On a regional scale, the build-up of salts by groundwater discharge and subsequent evaporation is considered to be the initial cause of saline soils (Magistad 1945, Purdy et al. 2005) which is consistent with the hydrology of

these sites. Each site is either in a regional groundwater discharge area or is affected by local saline springs. At the scale of a forest stand, the salinity of the groundwater and the height of the water table would both be expected to affect soil salinity. Because we monitored water table depth using wells, and not piezometers, we cannot differentiate between a perched water table and the main water table. We did observe perched water in the field during soil sampling; preferential flow from between the A and B horizons filled soil sampling pits with water from the top down.

Groundwater salinity was positively correlated with soil salinity at these sites, but the effect of water table level on salinity seemed more complicated. We expected that lower salinity plots would be the plots furthest from the water table, but the results did not support this idea at any of the aspen sites (Table 2.2). The high salinity plots had water table levels either lower than (Child Lake), or equal to (Zama Marsh) the medium and low salinity sites, or else the water table was below bedrock (Salt Pan Lake). Only at Clearwater and Benchmark was water table level clearly related to salinity level.

An obvious cause of correlations between groundwater chemistry and lower subsoil chemistry is saturation of the soil from a high water table. The lower subsoils at Clearwater, Child Lake, Zama Marsh, and at the high salinity level at Benchmark and Saline Lake were saturated sometime during the growing season of 2006. Where the water table was shallower than 1 m, correlations could be caused by capillary rise bringing groundwater to the soil profile. Very small rates of capillary rise are possible that can reach as high as 7 m above the water table (Ward and Robinson 2000).

Yarie et al. (1993) also found significant correlations between ions in river water, groundwater, and the soil solution. The influence of the groundwater on the soil chemistry of floodplains in interior Alaska may be similar to the influence of groundwater in saline landscapes of northern Alberta. In Alaska, vegetation played an important role in reducing the capillary rise of groundwater to the surface; the forests on naturally saline sites in Alberta could likewise exert some control over the movement of salts underneath them. Although evapo-transpiration by plants does increase the soil suction that draws capillary rise, the overall effect of vegetation seems to be decreased capillary rise, at least in semi-arid climates. An indirect effect of vegetation is the development of a forest floor or litter layer which can act as an evaporative barrier (Dyrness and Van Cleve 1993); reduced surface evaporation could lower soil suction and capillary rise (Ward and Robinson 2000). It is thought that vegetation also indirectly reduces soil evaporation by reducing wind speed and soil temperature at the soil surface (Dyrness and Van Cleve 1993, Yarie et al. 1993). Plants are known to lower the water table through interception and transpiration, and lowering of the water table would also reduce capillary rise because capillary flow is partially dependent on water table level (Van Cleve et al. 1993, Ward and Robinson 2000).

It seems that the ability of plants to reduce capillary rise of salts in the soils beneath them may be a critical factor allowing forest establishment on saline soils and that these forests may exist on a delicate balance of groundwater, precipitation, and temperature that creates a few decimeters of suitable substrate.

Highly saline groundwater, like the 77 dS/m water at Salt Plains, rising toward the surface could quickly deteriorate the growing conditions for most woody plants. Conversely, lower salinity groundwater near the surface, like the 5 dS/m water at Saline Lake, could provide much needed moisture for tree growth. However, if precipitation was low and vegetation did heavily draw upon groundwater for transpiration, increased suction forces could raise surface salts (Dyrness and Van Cleve 1993). Even 5 dS/m groundwater could quickly cause high salt accumulation in the topsoil, and possibly a surface salt crust if evapo-transpiration was very high. Surface salt crusts developed quickly on bare floodplains in interior Alaska during hot, dry weather (Dyrness and Van Cleve 1993) and also developed in the saline meadows of our study sites, sometimes not far from the forest edge. If surface salt concentrations fluctuated as drastically where forests were growing, the forests would probably die and be replaced by meadows dominated by halophytes.

2.5. Conclusions

In many ways the forests growing on these saline soils were quite ordinary. The understory species were typical of boreal forest stands. The overstory species were also typical of different successional stages and stand types of the boreal mixedwood. On saline soils, the potential exists for all stages of mixedwood successional development with a diversity of understory plant species.

If these sites were considered for timber production, 30% of the white spruce plots would not meet Alberta's current stocking standard of 800 live stems per hectare (Alberta Sustainable Resource Development 2006). Although the aspen and mixedwood plots all had ≥800 stems/ha, many of the stems in the highest salinity soil were small, leading to a low total and merchantable volume. Overall, the total volume of wood found on these saline sites spanned a range very similar to that found among a, b, d, and e ecosites dominated by jack pine, aspen, or white spruce on mostly non-saline soils in the oilsands region (Leskiw 2004); very low and very high volumes of wood are possible on saline soils. The chapters that follow will present forest productivity data in more detail, including discussing the effects of salinity beyond forest establishment – the effects over the lifetime of a tree.

Table 2.1. Location, ecosite classification (plant community type and ecological identification code) according to Beckingham and Archibald (1996), and land capability classification (soil moisture and nutrient regime) according to Leskiw (2006) of high (H), medium (M), and low (L) salinity plots at the study sites.

Site	Latitude	Longitude	Salinity Level	Plant community type	Ecological identification code	Soil moisture regime	Soil nutrient regime
Benchmark	59°47'36.73"N	111°57'37.90"W	H	Sw/feather moss	BM-d3.5/SM3	subhygric	Med-Rich
			M	Sw/feather moss	BM-d3.5/SM3	mesic	Med-Rich
			L	Sw/feather moss	BM-d3.5/SM3	mesic	Med-Rich
Clearwater	56°44'58.31"N	110°31'56.67"W	H	Sw-Sb/labrador tea/horsetail	BM-h1.1/SMp	subhygric	Med-Rich
			M	Sw-Sb/labrador tea/horsetail	BM-h1.1/SMp	subhygric	Med-Rich
			L	Sw/feather moss	BM-d3.5/SMp	subhygric	Med-Rich
Salt Plains	59°58'02.06"N	112°23'30.16"W	H	Sw/buffalo-berry	BM-d3.1/SM3	mesic	Rich
			M	Sw/buffalo-berry	BM-d3.1/SM3	subhygric	Rich
			L	Sw/feather moss	BM-d3.5/SM3	subhygric	Rich
Child Lake	58°25'31.73"N	116°32'24.54"W	H	Aw/saskatoon-pin cherry	BM-d1.2/SM4	mesic	Rich
			M	Aw/buffalo-berry	BM-d1.1/SM4	mesic	Rich
			L	Aw/buffalo-berry	BM-d1.1/SM4	mesic	Rich
Salt Pan Lake	59°49'15.03"N	112°00'36.22"W	H	Aw/saskatoon-pin cherry	BM-d1.2/SM4	mesic	Med-Rich
			M	Aw/buffalo-berry	BM-d1.1/SM1	submesic	Med-Rich
			L	Aw/buffalo-berry	BM-d1.1/SM1	submesic	Medium
Zama Marsh	59°06'09.1"N	118°03'42.4"W	H	Aw/saskatoon-pin cherry	BM-d1.2/SM4	subhygric	Rich
			M	Aw-Sw/buffalo-berry	BM-d2.1/SM4	subhygric	Rich
			L	Aw-Sw/buffalo-berry	BM-d2.1/SM4	subhygric	Rich
Saline Lake	57°04'27.64"N	111°31'29.89"W	H	Pb-Aw/dogwood/fern	BM-e1.1/SM3	subhygric	Rich
			M	Pb-Aw/dogwood/fern	BM-e1.1/SM3	mesic	Rich
			L	Pb-Aw/dogwood/fern	BM-e1.1/SM3	submesic	Rich

Table 2.2. Topsoil moisture content measured by EasyAg probes (at 10 cm depth in the mineral soil) and water table level measured by Odyssey probes (in cm below mineral soil) mean, minimum and maximum during the 2006 growing season at high (H), medium (M), and low (L) salinity plots at white spruce, aspen, and mixedwood sites. Wilting point (WP) and field capacity (FC) were estimated with particle size composition from equations by Saxton et al. (1986) and Pedosphere.com (2004). Groundwater electrical conductivity (EC) was measured midsummer 2006.

Dominant		Salinity	Volumetric Moisture (%)					Water Table Level (cm)			
Species	Site	Level	Mean	Min.	Max.	WP	FC	Mean	Min.	Max.	EC (dS/m)
White spruce	Benchmark*	H	42			11	26	41			36
		M	46			11	24	127			42
		L	30			10	28	>2.2			
	Clearwater	H	37	32	41			39	31	43	25
		M	41	39	44			53	38	63	6
		L	33	26	38			78	66	85	9
	Salt Plains	H	33	30	37	13	30	150	115	174	77
		M	39	30	47	9	25	143	126	162	52
		L	35	32	39	10	26	136	84	159	
Aspen	Child Lake	H	20	13	36	10	27	104	50	158	37
		M	19	9	30	13	27	83	1	139	11
		L	21	11	34	14	32	100	15	173	7
	Salt Pan	H	16	15	18	7	15		>133		
	Lake	M	13	6	28	7	14		>125		
		L	13	8	19	7	14	182	156	>200	7
	Zama Marsh	H	35	25	42	34	49	47	2	78	16
		M	40	27	69	34	49	43	3	83	13
		L	46	36	52	29	44	41	2	95	9
Mixedwood	Saline Lake	H	30	20	45	14	31	62	41	72	5
		M	36	27	50	16	32		>80		
		L	24	16	39	15	32		>74		

* Measurements were made only once in 2006

Table 2.3. Soil chemical properties: total carbon (C), total nitrogen (N), mineralizable nitrogen (Min.-N), carbon to nitrogen ratio (C:N), total cation exchange capacity (CEC) and exchangeable calcium and magnesium (Ex. Ca+Mg) of the forest floor (FF) and 0-20 cm mineral soil in high (H), medium (M), and low (L) salinity plots at white spruce, aspen, and mixedwood sites.

Dominant Species	Site	Salinity Level	Total C (T/ha)	Total N (kg/ha)	Min.-N (kg/ha)	C:N FF	C:N 0-20	Total CEC (eq/m^2)	Ex. Ca+Mg (eq/m^2)
White spruce	Benchmark	H	92	4719	43	31	17	36	19
		M	78	3979	68	37	15	26	15
		L	88	3915	85	25	21	47	28
	Clearwater	H	176	7630	143	26	22	-	-
		M	212	9482	90	27	21	-	-
		L	154	8111	107	25	17	-	-
	Salt Plains	H	82	7308	84	26	10	45	40
		M	157	10023	129	25	12	53	50
		L	172	10478	199	23	14	58	55
Aspen	Child Lake	H	135	12031	210	15	11	50	48
		M	53	4883	79	21	7	33	28
		L	61	5062	95	20	7	34	31
	Salt Pan Lake	H	83	5544	162	19	10	14	10
		M	72	5551	137	17	9	18	17
		L	68	5630	135	16	9	17	16
	Zama Marsh	H	159	12722	356	16	11	81	48
		M	130	9341	73	21	12	77	44
		L	91	6621	131	22	11	55	31
Mixedwood	Saline Lake	H	192	12737	442	17	15	71	69
		M	124	7668	321	17	16	51	49
		L	118	7037	321	17	17	51	50

Table 2.4. Significant ($\alpha = 0.5$) Spearman correlation coefficients between the groundwater and soil solution for the major ions, chloride to sulphate ratio ($Cl^-:SO_4^{2-}$), sodium absorption ratio (SAR), and electrical conductivity (EC) at the study sites.

Lower subsoil solution chemistry	Groundwater chemistry								
	Na^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}	$Cl^-:SO_4^{2-}$	SAR	EC
Na^+									
K^+									
Mg^{2+}			0.59						
Ca^{2+}									
Cl^-					0.62				
SO_4^{2-}						0.69			
$Cl^-:SO_4^{2-}$							0.90		
SAR								0.77	
EC									0.59

Table 2.5. The percent composition (density) and mean height of five dominant tree species in high (H), medium (M), and low (L) salinity plots at the study sites.

Site	Salinity Level	Aspen		White Spruce		Balsam Poplar		Balsam Fir		Paper Birch	
		%	Ht (m)	%	Ht (m)	%	Ht (m)	%	Ht (m)	%	Ht (m)
Benchmark	H	10	12.0	90	16.8						
	M	5	10.1	95	14.5						
	L	10	13.2	90	14.5						
Clearwater	H			90	13.7						
	M			80	14.9			10	4.4		
	L			16	18.0			20	7.1		
Salt Plains	H							84	6.5		
	M			100	9.8						
	L	9	13.2	100	15.6						
Child Lake	H	100	8.3	91	13.5						
	M	100	18.3								
	L	100	20.8								
Salt Pan Lake	H	95	10.4	5	10.4						
	M	85	12.8								
	L	80	16.9	5	5.2	15	9.3				
Zama Marsh	H	100	11.3			15	14.5				
	M	80	13.0	20	10.9						
	L	78	16.9	22	9.3						
Saline Lake	H	13	16.2	22	10.4	52	10.7				
	M	61	15.4	31	13.1	8	17.5			13	11.4
	L	67	13.7	33	17.3						

Table 2.6. Characteristics of white spruce, aspen, and mixedwood forest stands in high (H), medium (M), and low (L) salinity plots.

Dominant Species	Site	Salinity Level	Merchantable Volume* (m^3/ha)	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Live Stems (#/ha)	Snags (#/ha)
White spruce	Benchmark	H	157	241	25	667	133
		M	254	388	39	2200	400
		L	204	303	29	1000	200
	Clearwater	H	203	305	30	1000	0
		M	115	170	16	667	0
		L	162	236	15	1900	100
	Salt Plains	H	140	236	29	2200	500
		M	176	260	24	667	467
		L	151	233	25	1100	600
Aspen	Child Lake	H	28	61	9	2200	200
		M	243	363	37	1800	1500
		L	262	373	34	1400	200
	Salt Pan Lake	H	154	260	35	4300	1200
		M	119	182	21	1300	100
		L	263	384	39	2000	900
	Zama Marsh	H	62	103	14	800	1067
		M	243	380	45	2500	1100
		L	271	400	42	2700	1300
Mixedwood	Saline Lake	H	299	476	57	2300	1700
		M	258	378	38	1300	400
		L	343	480	42	1500	400

*Total volume minus the volume of tree tips (inside bark diameter < 2.0 cm) and tree stumps (height < 0.3 m)

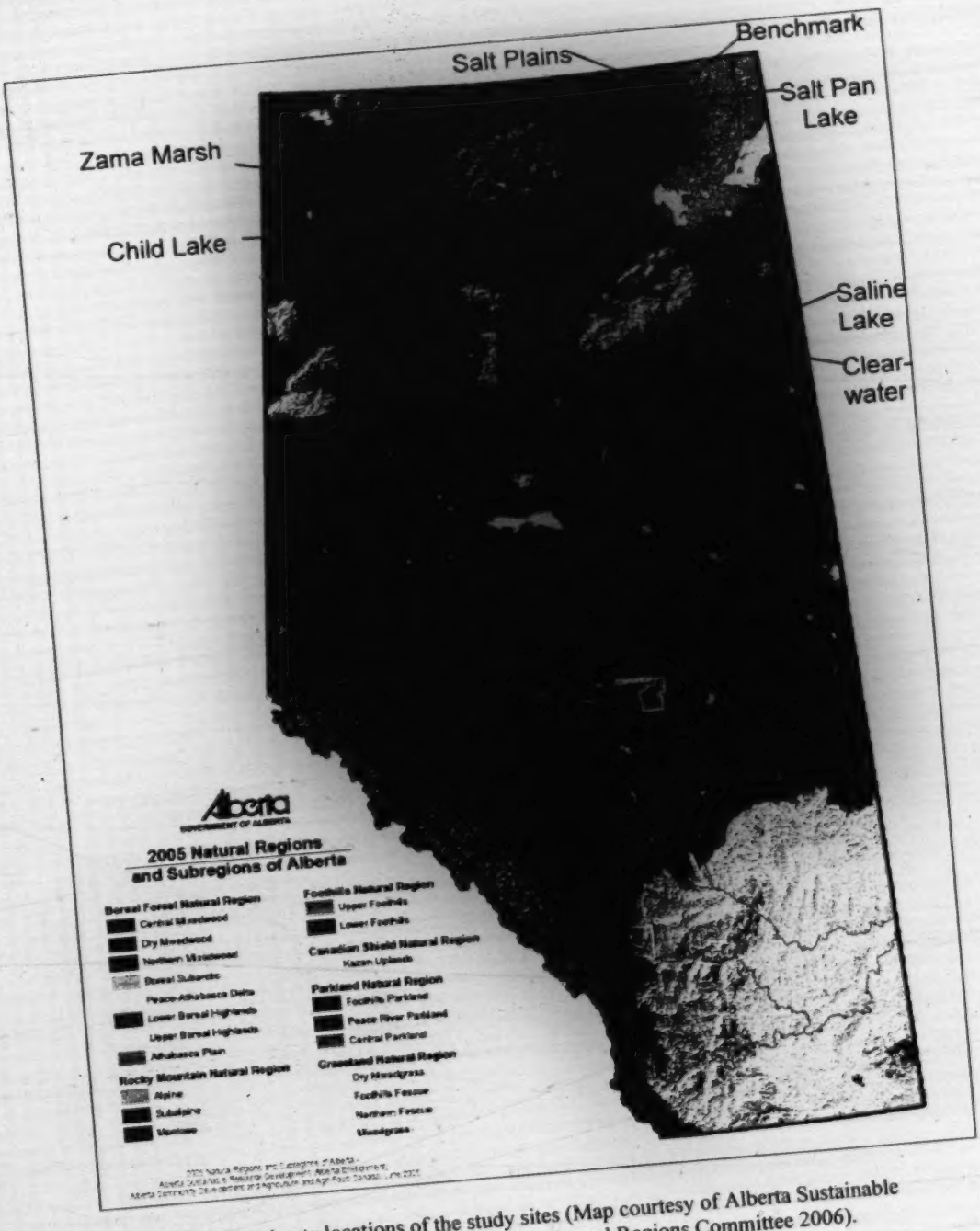


Figure 2.1. Approximate locations of the study sites (Map courtesy of Alberta Sustainable Resource Development for educational purposes; Natural Regions Committee 2006).

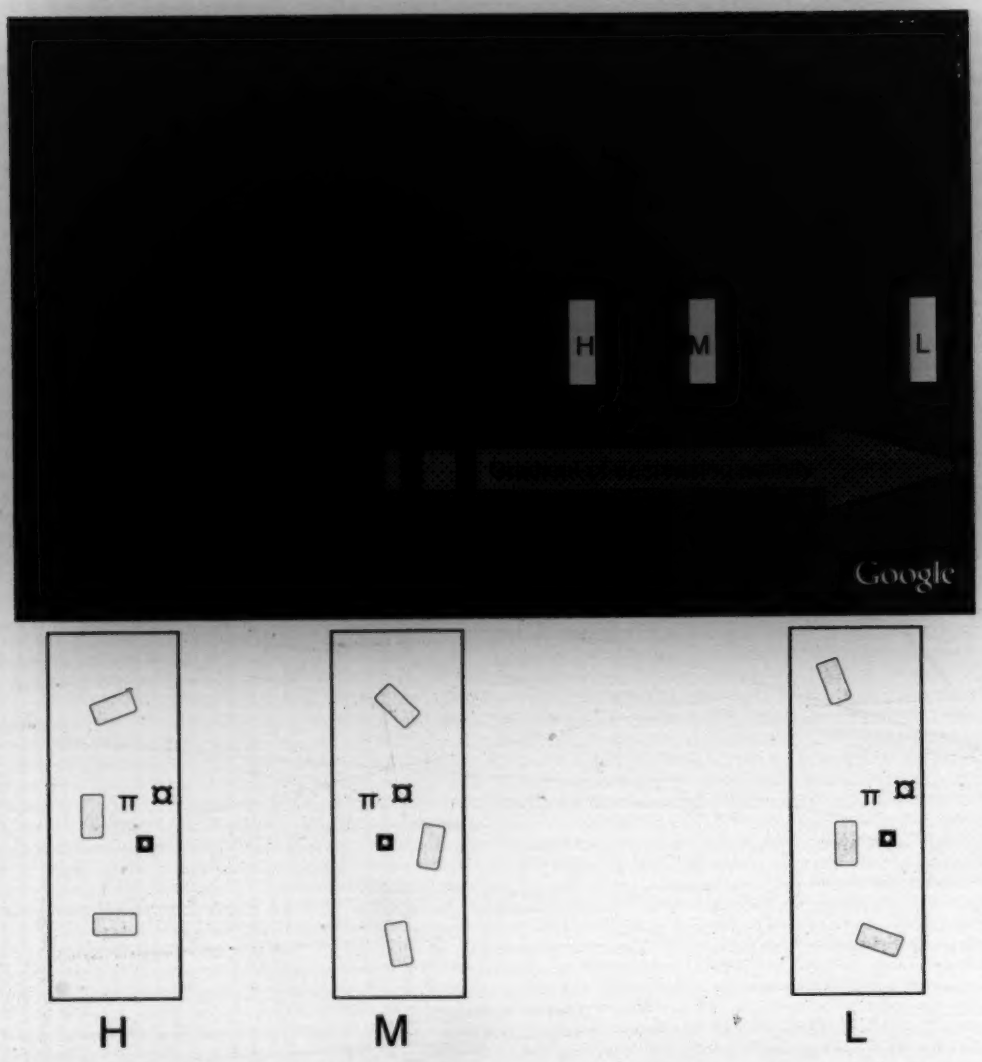
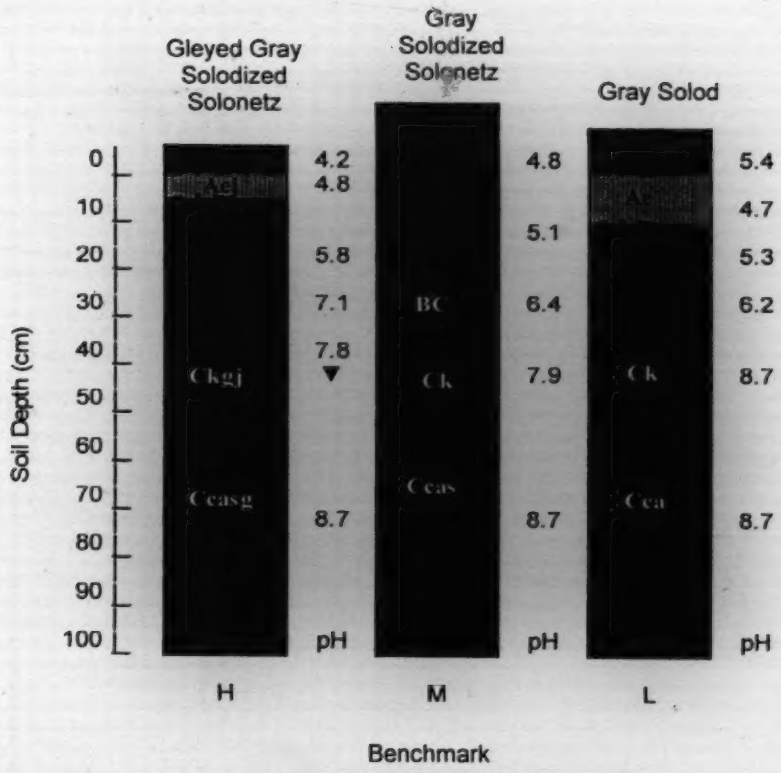


Figure 2.2. Diagram of plot set-up and approximate within plot sampling locations in high (H), medium (M), and low (L) salinity plots at Salt Pan Lake and their relationship to the open saline meadow and salt pan. Soil moisture (π), temperature (◘), and water table level (¤) probes were located centrally in each 5×20 m plot. Three soil sampling pits (gray rectangles) were evenly distributed within each plot. Satellite photo printed with permission of Google Earth mapping service.


Gleyed Gray Solodized Solonetz
Gray Solodized Solonetz
Gray Solod
Soil Depth (cm)
0
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90
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Ceasg
BC
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Ceas
Ck
Cca
4.2
4.8
5.8
7.1
7.8
8.7
4.8
5.1
6.4
7.9
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5.4
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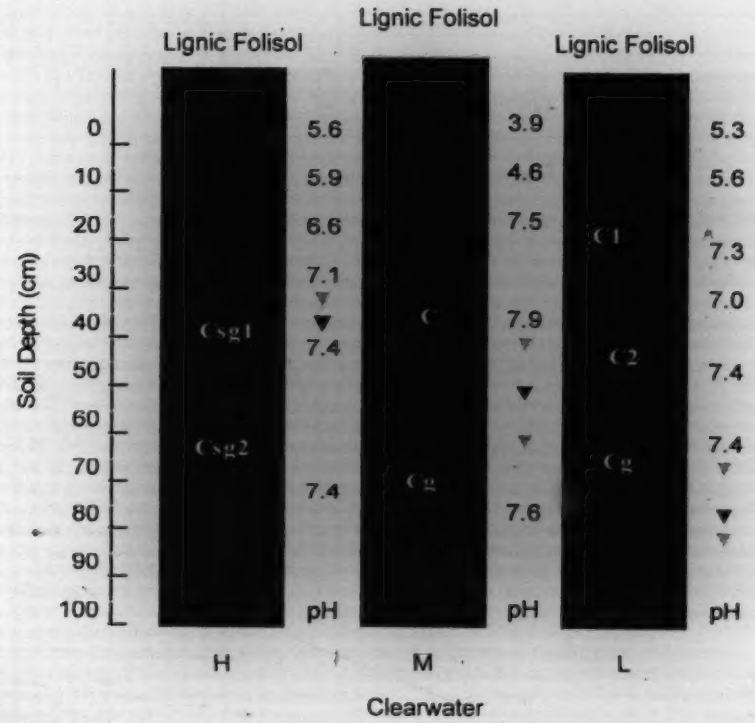
5.3
6.2
8.7
8.7
pH
H
M
L
Benchmark


Lignic Folisol
Lignic Folisol
Lignic Folisol
Soil Depth (cm)
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Csg2
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C1
C2
Cg
5.6
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7.1
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3.9
4.6
7.5
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7.4
pH
H
M
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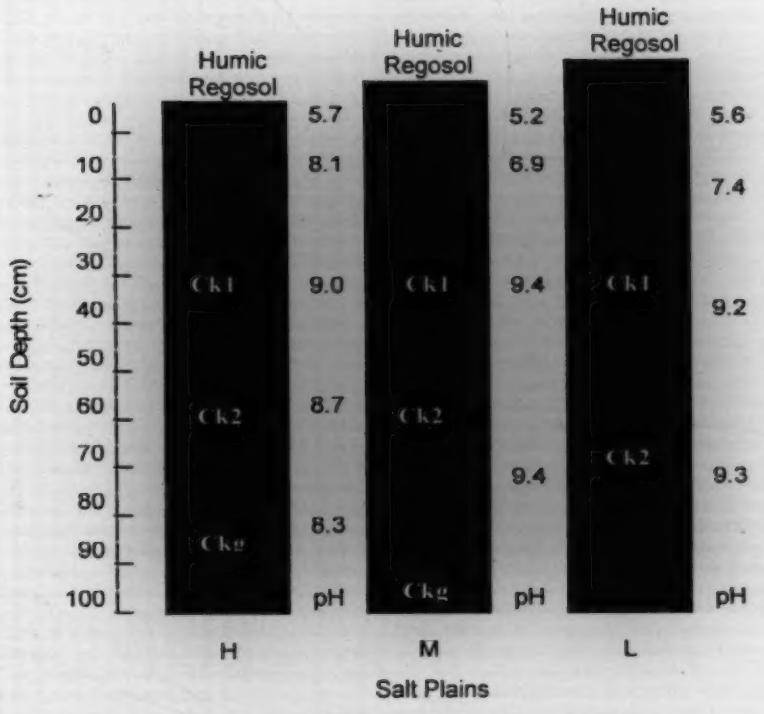
Clearwater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Humic Regosol
Humic Regosol
Soil Depth (cm)
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100
Ck1
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Ckg
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9.0
8.7
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pH
5.2
6.9
9.4
9.4
pH
5.6
7.4
9.2
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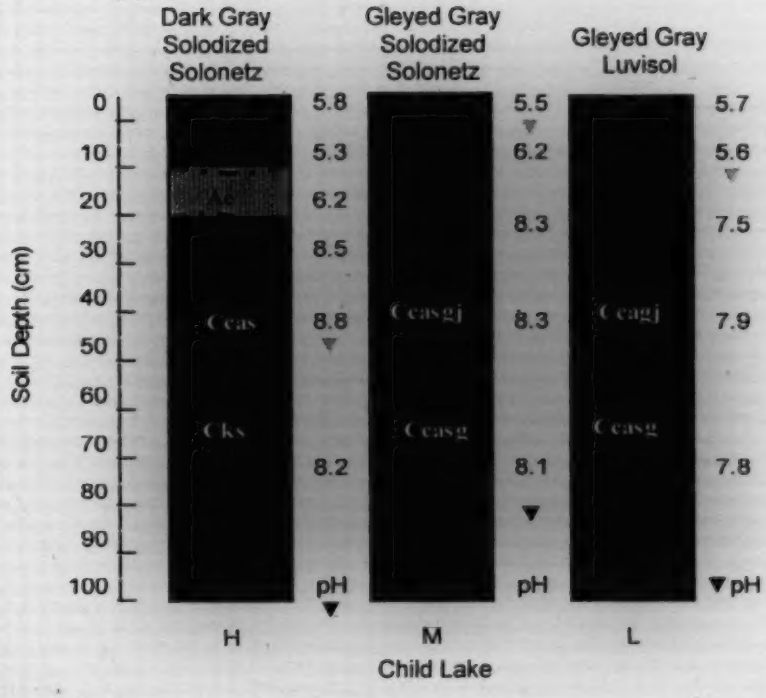
pH
H
M
L
Salt Plains


Dark Gray Solodized Solonetz
Gleyed Gray Solodized Solonetz
Gleyed Gray Luvisol
Soil Depth (cm)
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8.5
8.8
8.2
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6.2
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pH
5.7
5.6
7.5
7.9
7.8
pH
H
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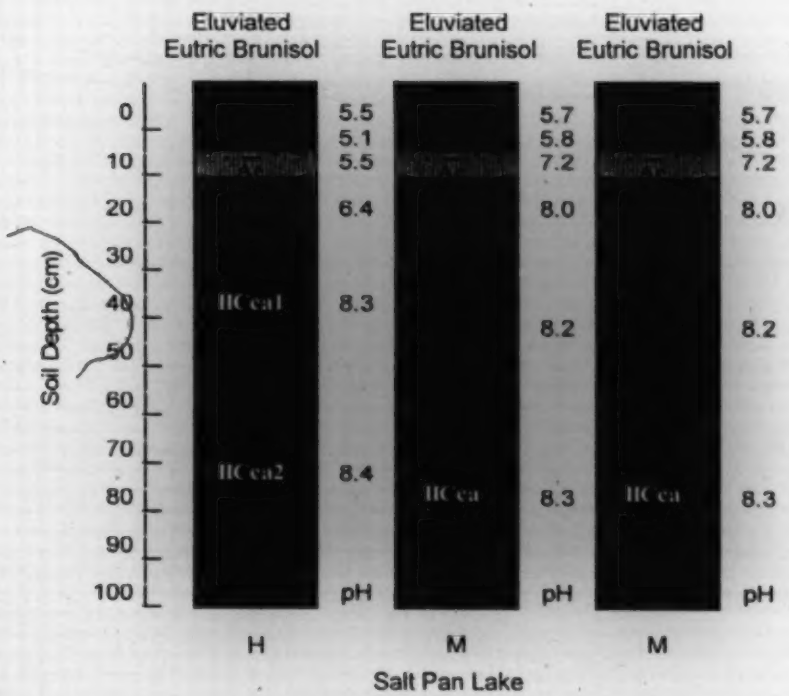
Child Lake


Eluviated Eutric Brunisol
Eluviated Eutric Brunisol
Eluviated Eutric Brunisol
Soil Depth (cm)
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IIC ca1
IIC ca2
IIC ca
5.7
5.8
7.2
8.0
8.2
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pH
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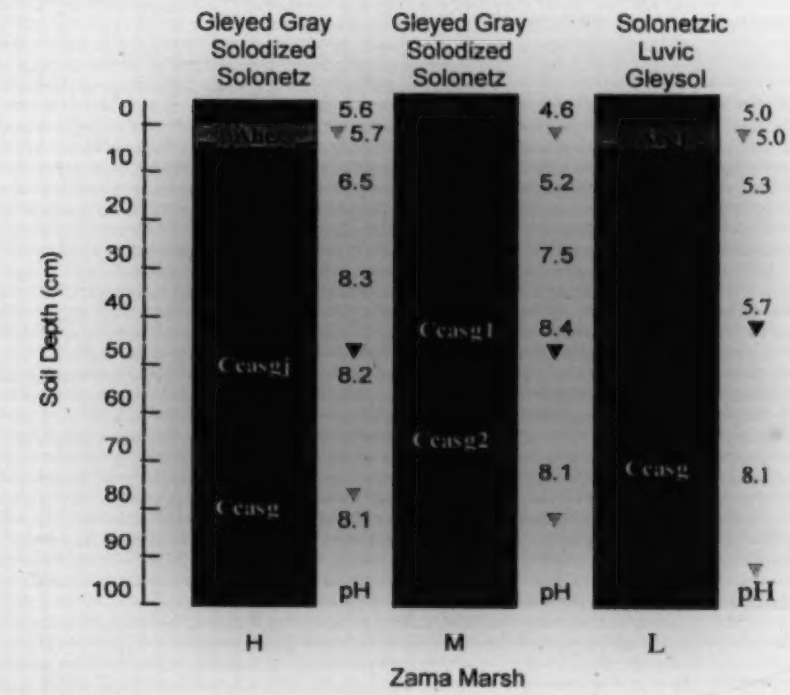
Salt Pan Lake


Gleyed Gray Solodized Solonetz
Gleyed Gray Solodized Solonetz
Solonetzic Luvic Gleysol
Soil Depth (cm)
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80
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5.6
5.7
6.5
8.3
8.2
8.1
pH
Ccasgj
Ccasg
4.6
5.2
7.5
8.4
8.1
pH
Ccasg1
Ccasg2
5.0
5.0
5.3
5.7
8.1
pH
Ccasg
H
M
L
Zama Marsh

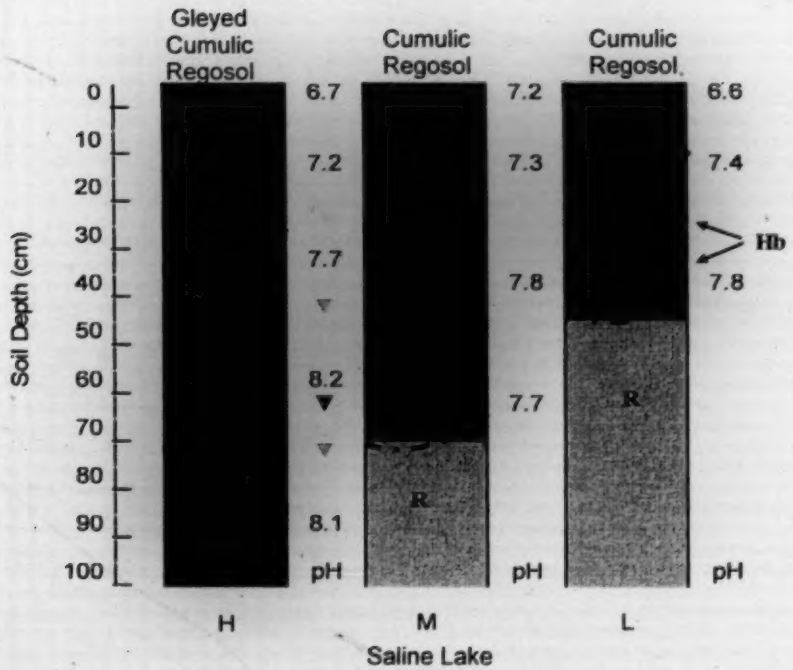

Figure 2.3. Soil classification (Soil Classification Working Group 1998, Fox et al. 1987) and soil horizon designations along a salinity gradient (high [H], medium [M], and low [L] salinity plots) at the study sites. Inverted triangles indicate the mean (black) and range (gray) of water table depth for plots at which depth to groundwater was less than 100 cm in 2006.

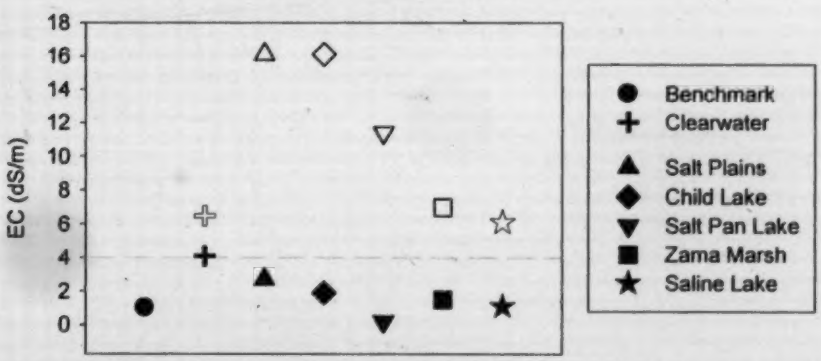

Figure 2.4.Comparison of topsoil electrical conductivity between the forest ("inside"; solid symbols) and the adjacent unforested saline area ("outside"; open symbols) at each site. Reference line is at 4 dS/m.

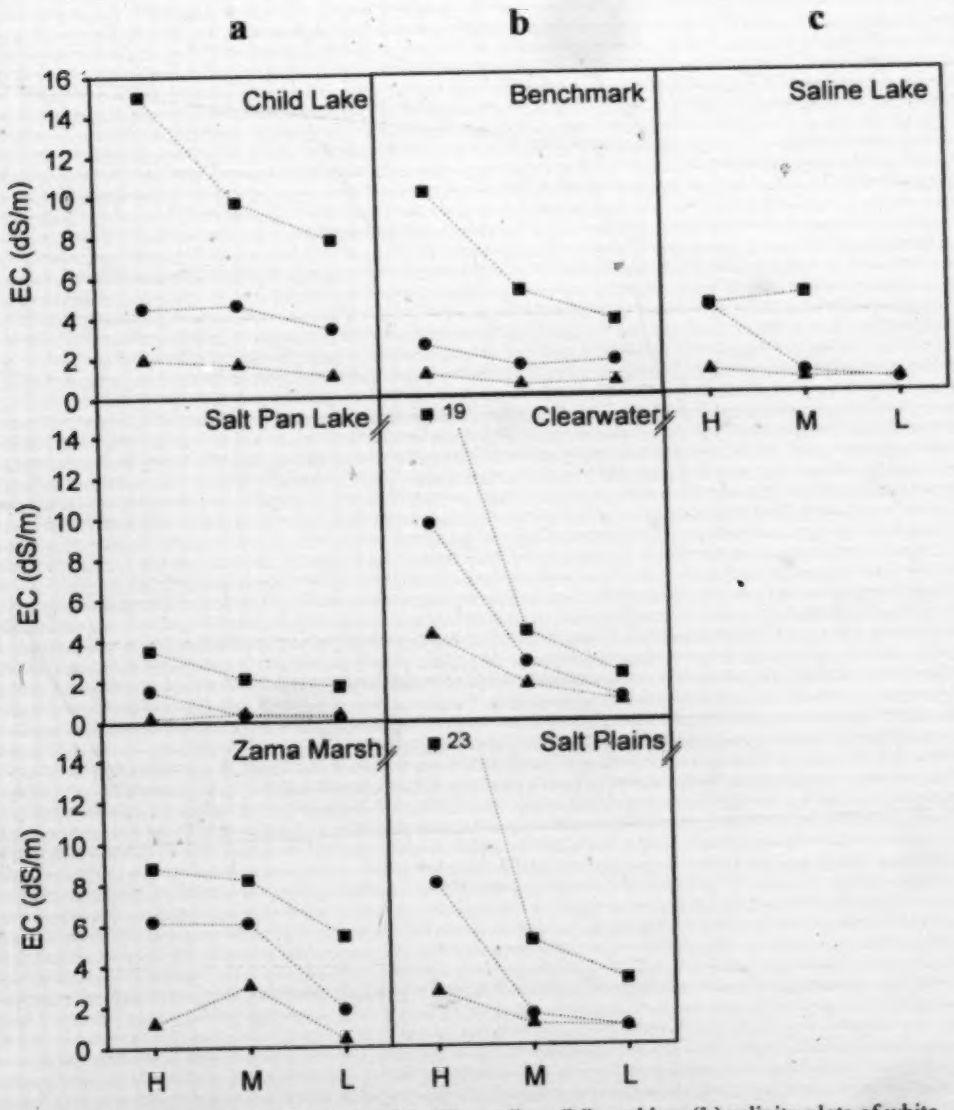

Figure 2.5. Electrical conductivity in high (H), medium (M), and low (L) salinity plots of white spruce stands (a), aspen stands (b), and one mixedwood stand (c) in the lower subsoil (squares), upper subsoil (circles), and topsoil (triangles). Reference line is at 4 dS/m.

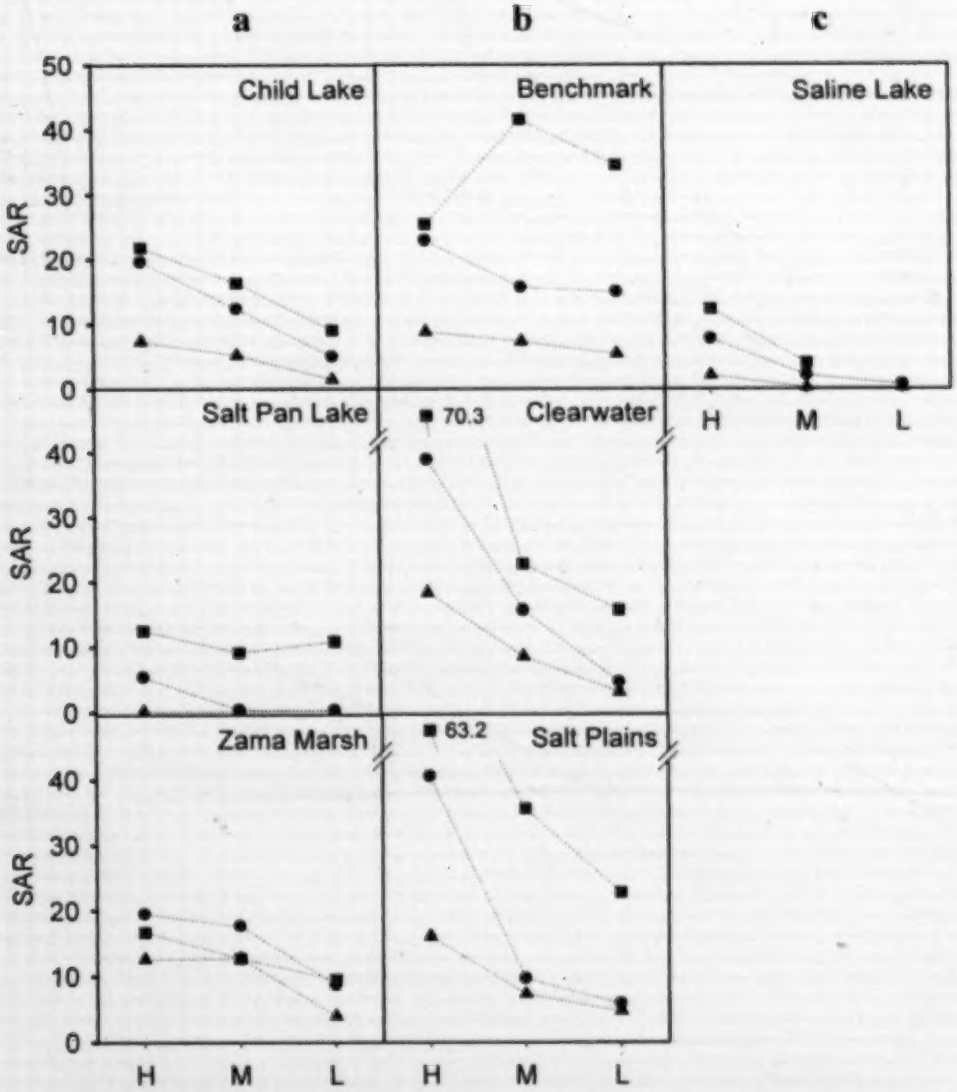

Figure 2.6. Sodium absorption ratio for the topsoil (triangles), upper subsoil (circles), and lower subsoil (squares) of high (H), medium (M), and low (L) salinity plots at white spruce (a), aspen (b), and mixedwood sites (c). Reference line is at 13, above which a soil is considered sodic.

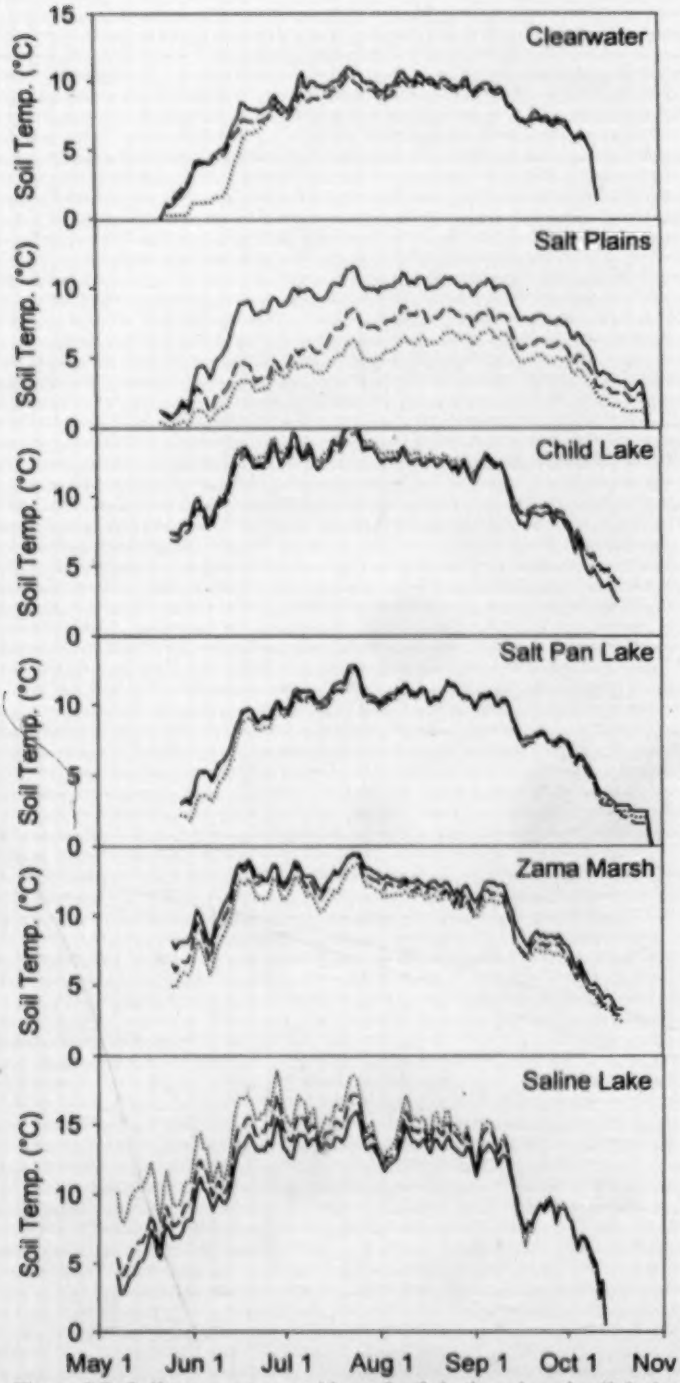

Figure 2.7. Soil temperature at 10 cm depth in the mineral soil during the 2006 growing season in high (solid lines), medium (dashed lines), and low (dotted lines) salinity plots at the study sites.

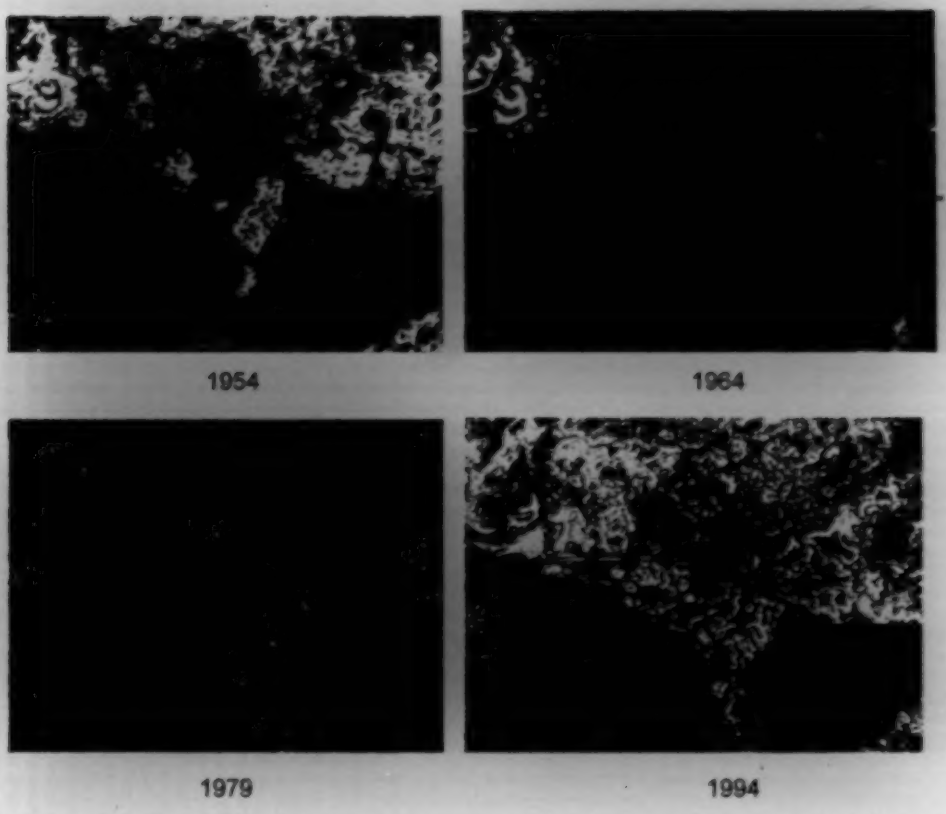

Figure 2.8. Aerial photo series of changes in water level and surface salt crusts (white areas) in the saline wetlands (portion of photographs above the drawn lines) of the Zama Marsh site. Photos printed with permission of Alberta Sustainable Resources Development, RIMB, Air Photo Distribution.

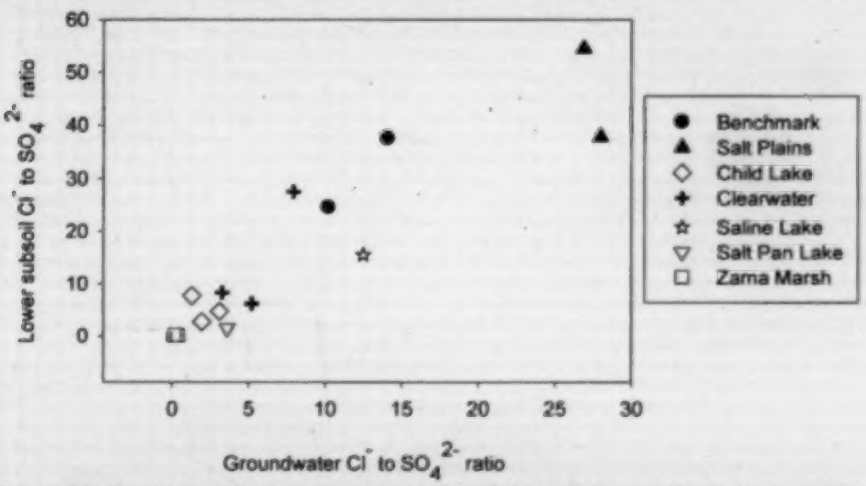

Figure 2.9. Correlation (Spearman correlation coefficient = 0.90, $p < 0.05$) between the chloride to sulfate ratio in the groundwater and lower subsoil solution (depth of 50-100 cm) along salinity gradients at white spruce sites (closed symbols) and aspen and mixedwood sites (open symbols). Sites above the reference box for a 1:1 chloride to sulfate ratio are dominated by chloride.

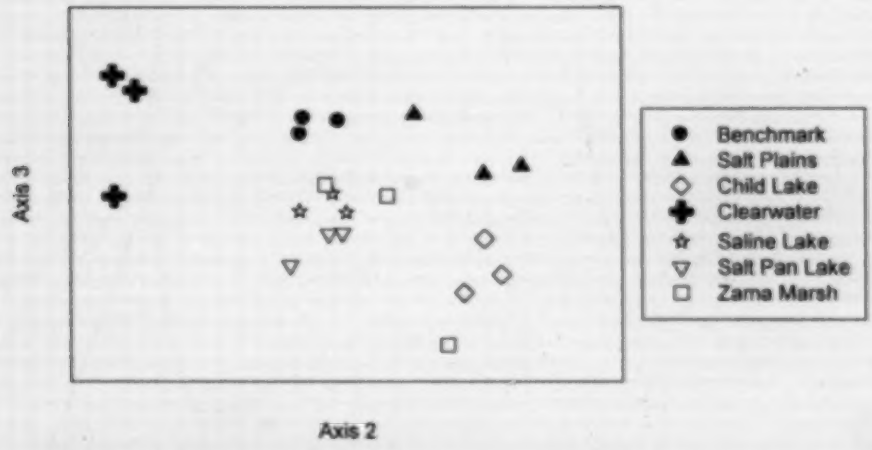

Figure 2.10. Nonmetric multidimensional scaling ordination of understory vascular plant community composition at white spruce sites (closed symbols) and aspen and mixedwood sites (open symbols). A 3-dimensional solution was determined to be the best for these data. This solution had a stress of 9.4 and instability < 0.000001 after 67 iterations.

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Chapter 3. The effects of soil salinity on mature aspen

3.1. Introduction

Aspen is the most abundant deciduous tree species in the boreal forest, and the most widespread tree across North America (Rowe 1972). In western Canada, aspen is an important species for the forestry sector. Many pulp and paper operations rely on aspen for fiber supply including companies in north-eastern Alberta in the oilsands region. For future fiber production, and to meet government regulations and societal expectations, it is desirable that reclaimed landscapes after oilsands mining support forests equivalent in productivity to those that were lost during mining. To meet these demands, oilsands mining companies hope that salt-affected soils will support merchantable aspen forests.

Aspen is not known to be exceptionally salt tolerant. In one study, every aspen seedling growing in a salinity treatment died before the end of the experiment (Khasa et al. 2002). However, aspen is known to tolerate drought (Abrams 1988), which suggests that it might also be able to survive water deficit caused by salinity. Aspen may have an advantage over evergreen species in saline soils because it is deciduous and if ions accumulate to harmful levels in leaves, leaves can be shed and regrown (Renault et al. 1999). Although physiologically costly, growing new leaves with lower ion concentrations could prevent plant death. Aspen's ability to grow quickly after disturbance (Perala 1990) may not be an advantage in saline soils where slow growth can be a mechanism for salt-tolerance (Khasa et al. 2002). The degree to which aspen withstands water deficit, ion toxicity, or both, over long time periods in the field will probably be an important factor in aspen productivity on saline soils.

In the past, carbon stable isotope ratios have been used to assess water stress in many different species and these could be a useful tool for quantifying salinity-induced water stress in aspen. Carbon stable isotope ratios in plant tissues integrate processes related to photosynthesis and transpiration over the time period that the tissue developed (Robinson et al. 2000). Environmental stresses, including salinity, can affect the discrimination against the heavier isotope, ^{13}C, during photosynthesis; in C3 plants, Rubisco[1] discriminates strongly against ^{13}C during carbon fixation, but if the internal concentration of CO_2 declines under stress, due to stomatal closure, discrimination decreases (Robinson et al. 2000). To prevent water loss, plants under increasing water stress due to salinity are thought to reduce stomatal conductance, leading to lower amounts of within plant CO_2 and thus lower carbon isotope discrimination (Farquhar et al. 1989). Plants grown on a common source of CO_2 would therefore have increasing ^{13}C in their foliage with increasing water stress. Increasing water stress due to salinity has been documented with carbon stable isotope ratios in *Puccinellia nuttalliana* (Schultes) A.S. Hitch. (Guy et al. 1986), a halophyte common in the saline meadows of the boreal forest, but to our knowledge, not in aspen.

[1] ribulose-1,5-bisphosphate carboxylase/oxygenase, the primary carbon capture enzyme

Nutrient stress could also affect aspen growing in saline soils. Whether by water deficit or ion excess, salinity can alter the concentrations or ratios of essential nutrients in tissues, potentially causing nutrient deficiencies or toxicities (Grattan and Grieve 1993). Foliar nutritional status has been linked to plant productivity in numerous species, including aspen (Chen et al. 1998); salinity effects on nutritional status could thus affect aspen growth. Nutrient limitation, especially of P and N, is an important control on aspen seedling growth in Alberta plantations (van den Driessche et al. 2003, 2005) and could be a factor in saline soils as well. Aspen is known to quickly exploit fertile sites in the boreal forest and has the potential to greatly increase productivity with the addition of limiting nutrient(s) (Chapin et al. 1983, 1986). Because management practices on reclaimed salt-affected soil could include fertilization, information about limiting nutrients and interactions between salinity and nutrient uptake would be valuable for reclamation planning and management.

Nitrogen is often a limiting nutrient in forest soils, so any effect of salinity on nitrogen uptake and assimilation could have consequences for forest productivity. The nitrogen stable isotope ratios of tree foliage can provide information about plant nitrogen sources and nitrogen limitation beyond that provided by simple measurements of foliar nitrogen concentration. The amount of ^{15}N in a plant reflects the amount of ^{15}N of the source and any ^{15}N discrimination, nitrogen gains and losses, and/or nitrogen pool mixing as plant tissues develop (Robinson 2001). Drought stress has been shown to affect ^{15}N in *Hordeum vulgare* L. (Robinson et al. 2000), and nutrient stress affected ^{15}N in white spruce seedlings (Pritchard and Guy 2005). By integrating a number of ecosystem and physiological processes, foliar $\delta^{15}N$ (the relative amount of ^{15}N in comparison with the atmosphere) can be another means to assess the effect of salinity on aspen growth and nutritional status.

Ion toxicity has been well documented as a mechanism through which salinity affects vegetation in the boreal forest, including aspen (Rowell and Crepin 1977, Edwards and Blauel 1975, Renault et al. 1999). The degree to which ion toxicity affects aspen growing in saline soils, and the concentration of ions in the soil solution that aspen can withstand without leaf damage, are probably important indicators of its salt-tolerance (Allen et al. 1994). Genotype can also be a factor affecting growth, and intra-specific variation in growth response to soil salinity could mean that selective propagation might improve salt tolerance in aspen; differences in growth among clones in saline conditions have already been documented in a laboratory experiment (Khasa et al. 2002), but have not been investigated in the field.

Extensive research in agriculture and plant physiology has examined interactions between plants and salinity related to water stress, nutritional status, and ion toxicity, but little of this research has been on trees, and even less on mature trees. The lifespan of a plant physiology experiment is generally far shorter than it takes to grow a tree, especially at northern latitudes. Because species can differ substantially in salt tolerance, species-specific information is vital for the successful use of species in oilsands revegetation, including aspen. In this study we were fortunate to locate mature stands of aspen growing naturally in

different levels of salinity. We took advantage of the aspen dominated salinity gradients, as described in Chapter 2, to examine the long-term effects of salinity on aspen growth and physiology. The information from this study will help us understand how future forests might develop on salt-affected soils in the oilsands region, and give us more information about how the soil characteristics of saline sites relate to aspen growth.

The objectives of this study were (*i*) to examine the relationship between aspen growth and soil salinity; (*ii*) to understand whether salinity caused water stress in aspen; (*iii*) to investigae whether salinity affected nutritional status or nitrogen uptake in aspen; and (*iv*) to explore the relationship between salinity and salt ion accumulation in aspen foliage. The influences of environmental factors other than salinity on aspen growth and physiology were also investigated.

3.2. Methods

3.2.1. Site description and plot set-up along the salinity gradient

The sampling for this study was conducted at naturally saline sites in northern Alberta with forests dominated by aspen: Child Lake, Salt Pan Lake, and Zama Marsh (Table 2.1, Figure 2.1). At each site there was a distinct boundary between forest vegetation and vegetation dominated by grasses and shrubs. This boundary corresponded with a decrease in the electrical conductivity of the topsoil from above 4 dS/m (grass and shrub vegetation) to below 4 dS/m (forest vegetation; Figure 2.4). We located a transect of decreasing salinity from the forest edge to the forest interior at each site and identified appropriate locations for 5×20 m^2 sampling plots at high, medium, and low salinity levels (Figure 2.2). High, medium, and low salinity plots were based on relative differences in the conductance of the parent geologic material (PGM) within each site, measured with an EM-38 (Geonics Ltd., Mississauga, Ont., Canada). At each site the high salinity plot was located adjacent to the forest edge (the limit of salinity tolerance for trees at each site) and the low salinity plot was located where the least saline soils were found at the site. Salinity varied with depth in the soil profile at each site and the levels of salinity varied among sites. As such the 'high', 'medium', and 'low' levels of salinity were only relative to each other within a site and not between sites. We hereafter refer to the three locations along the salinity gradient at each site simply as 'high', 'medium', and 'low' because there was no single quantitative measure of salinity in any plot. The electrical conductivity (EC) throughout the soil profile was measured once in each plot, generally confirming that soil salinity decreased from the high to the low salinity plots, and that the absolute EC differed among sites (Figure 2.5).

Each site had saline soils, but many other soil characteristics differed among sites. Soils at Child Lake were Dark Gray Solodized Solonetzes, Gleyed Gray Solodized Solonetzes, and Gleyed Gray Luvisols, in the high, medium, and low salinity plots, respectively. Soils at Salt Pan Lake were Eluviated Eutric Brunisols along the entire salinity gradient. Soils at Zama Marsh were Gleyed Gray Solodized Solonetzes in the high and medium salinity plots, and Solonetzic

Luvic Gleysols in the low salinity plot (Figure 2.3; Soil Classification Working Group 1998). Water table level also differed among sites with a mean depth between 83 and 104 cm at Child Lake, between 41 and 47 cm at Zama Marsh, and greater than 125 cm at Salt Pan Lake (Table 2.2). The understory vascular plant community at each site was typical of aspen forests in northern Alberta.

3.2.2. Tree sampling

Four trees per salinity level were selected for sampling using a stratified random sampling method. Trees were stratified by canopy dominance and health; candidate trees were dominant canopy trees not overtopped by a neighboring stem, free from disease, damage, or rot, and safe to fell. Two trees that met these criteria were randomly selected to be felled for stem analysis and two additional trees were cored twice with an increment borer at 1.3 m in height for tree ring analysis. The diameter and height were measured on all trees in each 100 m^2 plot. A few of the felled trees were located just outside of the 5×20 m plot, within which we performed the soil sampling and stand measurement.

During tree felling, stems were cut somewhere between 0.3 m (stump height) and 1.3 m (breast height). After felling, stem length was measured and stem cross-section samples (tree cookies) were cut and collected at 1.3 m, 2.3 m, 3.3 m, and every meter thereafter until the top. A cookie was also cut and collected at stump height (0.3 m). Tree cookies were oven dried at 65 °C and the diameter at 1.3 m was remeasured to adjust future calculations for shrinkage. Diameters decreased 6% during oven drying. Tree cores were air dried and mounted onto wooden blocks. All samples were then sanded with progressively finer grades of sandpaper, ending with 600 grit, so tree rings could be seen clearly.

A dissecting microscope was used to view tree rings and cross date all samples within a site (Yamaguchi 1991). Each sample was dated along 2 radii to ensure correct ring counting.

3.2.3. Ring width measurement

Ring widths were measured on the breast height samples – two cookies and two cores per salinity level per site. A Velmex microscope-sliding stage system (Velmex Inc., Bloomfield, NY, USA) was used to measure tree ring widths. The inner and outer radius of each ring was measured on two average radii per sample to increase the accuracy of ring width measurement and used to calculate the area of wood in each ring, or the basal area increment (BAI) using the equation:

$$BAI = \pi(R^2_n - R^2_{n-1})$$

where R is the tree radius and n is the year (Kolb and McCormick 1993, Hogg et al. 2002). Tree ring widths decrease with tree age because circumference increases; calculating the BAI is one way to account for that change, enabling comparison of growth rates in trees of different ages. BAI is expressed as area before drying. It took 5-10 years of growth beyond breast height age for the BAI

of juvenile trees to reach the average BAI level of older trees, so to compare trees at all sites to each other, the 1990's was the only decade with a full sample set (some high salinity trees at Child Lake only reached breast height in 1984). The BAI was averaged across the ten years from 1990 to 1999 inclusive for each tree so that a single (mean) value of basal area growth per year for each tree was used in subsequent analyses.

Basal area growth data were analyzed with ANOVA using the following model:

$$Y_{ijk} = \mu + \text{Site}_i + \text{Treatment}_j + \text{Treatment}\times\text{Site}_{ij} + e_{k(ij)}$$

where Y_{ijk} is the k^{th} tree in the j^{th} site of the i^{th} salinity level, which is equal to the overall mean (μ), plus the effect of the i^{th} site (Child Lake, Salt Pan Lake, or Zama Marsh), the j^{th} treatment (high, medium, or low salinity), the interaction of the i^{th} site and the j^{th} treatment, and the random error among trees within a treatment at a site ($e_{k(ij)}$). Both 'Site' and 'Treatment' were considered fixed effects. The general linear model procedure in the SAS software package (v 9.1; SAS Institute Inc., Cary, NC, USA) was used to analyze the data. Basal area increment data were square-root transformed before analysis to meet the assumptions of ANOVA, but the untransformed data are presented in this chapter. When there were significant effects in the model at $\alpha = 0.05$, least squared means were compared with a comparison-wise $\alpha = 0.05$.

3.2.4. Stem analysis

After cross-dating, the age and height in the tree were recorded for each tree cookie. The age at breast height (BH age) was used because of the difficulty in obtaining the absolute age in the boreal forest (Gutsell and Johnson 2002, Peters et al. 2002). To account for the problem in stem analysis of underestimating the actual tree height at a given age, we adjusted the data with Carmean's (1972) algorithm for each tree separately (Dyer and Bailey 1987, Chen et al. 2002). These data were plotted to create age-height growth curves for each tree, which were then compared visually to provincial average growth curves for aspen in Alberta (Huang et al. 1994). Site index (height at 50 years breast height age) was calculated from these curves, using the equation for a straight line between the age-height points on either side of 50 years old, and averaged for the two trees in each plot. Site index could not be calculated for the high salinity level at Child Lake because those trees were less than 50 years old when felled. No statistical analysis was performed on stem analysis data because of the small sample size (2 trees per plot).

3.2.5. Foliage sampling and analysis

Leaves were collected from four aspen trees in each plot in the summer of 2006. Aspen at Zama Marsh had been defoliated by forest tent caterpillar in early summer, so leaves were collected in August after regrowth. For the felled trees at Zama Marsh, the foliage was collected from the top third of the crown. For all other trees, foliage was collected with a pruning pole from as high as possible in

the crown, or by shaking the stem hard enough for small twigs and branches (with leaves attached) to fall off. We collected as many leaves as we could from each tree. Leaves were air dried and 100 leaves were counted for each tree. When less than 100 leaves were collected, we counted all leaves collected from the tree. Salt Pan Lake aspen also had a forest tent caterpillar outbreak in 2006 so collected leaves were assessed for percent damage. All leaves were oven dried at 65 °C, weighed, ground with a Wiley mill, and then sub-sampled and finely ground with an electronic ball grinder.

The foliar concentrations of Na, macronutrients (P, K, Ca, Mg, and S), and micronutrients (Mn, Fe, Al, Zn, and Cu) were determined by the Analytical Services Laboratory at the Northern Forestry Centre in Edmonton, Alberta. Samples were digested with a CEM (Matthews, NC, USA) MARS Xpress microwave digestion system and then measured on a Spectro (Kleve, Germany) Cirrus Inductively Coupled Plasma Atomic Emission Spectrophotometer. Extractable foliar Cl concentration was determined by ion chromatography (DI 300; Dionex Corporation, Sunnyvale, CA, USA) on filtered water samples obtained by combining two successive 1-hr extractions of 0.05 g samples with hot water (Franklin and Zwiazek 2004). Foliar C and N concentrations were determined by the Dumas combustion method on a Carlo Erba (*now* CE Elantech Inc., Lakewood, NJ, USA) NA1500 Elemental Analyzer (Carter 1993). All foliar elemental concentrations were expressed on a per dry weight basis, and were compared to previously-published values for aspen and closely related species.

$\delta^{13}C$ and $\delta^{15}N$ were determined using a Finnigan Delta Plus Advantage isotopic ratio mass spectrometer (Thermoquest, Bremen, Germany) with a ConFlo III universal interface. A Costech (Valencia, CA, USA) ECS 4010 elemental analyzer was used as a peripheral to combust the samples according to the Dumas method (Carter 1993). Stable isotope composition is expressed as a ratio relative to Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen according to the equation:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = 1000 \times (R_{sample}/R_{standard} - 1)$$

where R is the abundance ratio of the heavier isotope to the lighter isotope (Dawson et al. 2002).

Data for each variable measured on the foliar samples were analyzed with ANOVA using the same general linear model as for the basal area increment data. Variables that did not meet the homogeneity of variance assumption of ANOVA (Cl, S, $\delta^{15}N$) were square root transformed, and then analyzed. After transformation, foliar sulphur and $\delta^{15}N$ still did not meet the assumptions, so the original data were analyzed with the mixed procedure in the SAS software package, and the heterogeneous variances were compensated for in the model (SAS Institute Inc.). In all cases, the original, untransformed data are presented in this chapter. Some of the data did not meet the assumption of normality, but none were severely non-normal, so ANOVA was still used. Forty-eight comparisons were made (3 tests for 16 variables) on the foliar samples; to retain an experiment-wide alpha of 0.05, we made a Bonferroni adjustment and differences

were only considered significant at the $\alpha = 0.001$ level. This adjustment in alpha also improved the likelihood that statistically significant results were also biologically meaningful. When a significant effect of site, treatment, or a site by treatment interaction was found, the least squared means for the appropriate effect were compared, also at $\alpha = 0.001$.

3.2.6. Soil sampling and analysis

Soils were sampled in 2005. In each plot we dug three soil pits: one central soil pit, and pits between the center and each plot end (Figure 2.2). We sampled the soil by horizon and bulked the corresponding soil samples from each pit into one sample per horizon for each plot. In the laboratory, all samples were air dried and ground to pass through a 2 mm sieve. Soluble Cl^- and SO_4^{2-} concentrations were measured on saturation extracts (Sparks 1996) by ion chromatography with a DX600 (Dionex Corp., Sunnydale, CA, USA). In order to make comparisons among sites that had different horizons we calculated weighted Cl^- and SO_4^{2-} concentrations by depth for three depths: topsoil (0-20 cm), upper subsoil (20-50 cm) and lower subsoil (50-100 cm).

Cation exchange capacity (CEC), and exchangeable Ca^{2+}, Mg^{2+}, and Na^+ were determined only in mineral soil horizons within 20 cm of the forest floor. For soil samples without carbonates (pH> 7.0 or exch. $Ca^{2+} + Mg^{2+} + Na^+ + K^+ >$ total CEC) exchangeable and soluble cations were extracted with 1M NH_4Acetate at pH 7.0 and determined with a SpectrAA 880 (Varian Inc., Mississauga, Ont., Canada) Atomic Absorption Spectrometer. The soluble cations, as determined from the saturation extract, were subtracted from the total exchangeable and soluble cations to calculate exchangeable Ca^{2+}, Mg^{2+}, and Na^+, as recommended by the US Salinity Laboratory Staff (Richards 1954). Total cation exchange capacity (CEC) was measured with an NH_4Acetate extraction and displacement of NH_4^+ with Na^+ (McKeague 1978). Displaced NH_4^+ was determined by autoanalyzer colorimetry with an AutoAnalyzer II (Technicon Instruments Corp., Tarrytown, NY, USA). Exchangeable cation ratios were calculated as the ratio of the exchange capacity filled by one base cation to the remaining cation exchange capacity with the equation:

$$\text{Exchangeable Sodium Ratio} = \text{ex. } Na^+ / (\text{Total CEC} - \text{ex. } Na^+) \text{ (Richards 1954)}$$

This was done for calcium, magnesium, and sodium separately. Exchangeable cation ratios for each site were the mean ratios of plots within a site, calculated using exchangeable cation ratios for each horizon along with the horizon depth. We have no data on within plot variation in soil properties because soil samples were bulked into one sample per horizon per plot.

3.3. Results and discussion

3.3.1. Salinity effects on aspen growth

The mature aspen growing on naturally saline soils in this study showed the same response to soil salinity as that of aspen and hybrid poplar seedlings in experimental field (McKenzie et al. 1993) and greenhouse (Khasa et al. 2002) trials. The lowest aspen basal area growth rate occurred at the highest salinity level at every site (Figure 3.1; $p = 0.0001$ for the effect of treatment). At Child Lake and Salt Pan Lake, the highest BAI was at the low salinity level, although at Zama Marsh the highest BAI was at the medium salinity level (Figure 3.1). At all sites, aspen in the high salinity soils were growing between 2.2 and 3.2 cm^2/year, or about 50% of the 4.5 to 6.2 cm^2/year growth achieved by the aspen growing in the lower salinity soils (Figure 3.1). The lower growth rates were similar to growth rates in pest- and pathogen-stressed aspen stands near Grande Prairie, Alberta from 1990-1998 (~2.7 cm^2/year; Hogg et al. 2002). The fastest growth rates were higher than growth rates in healthy aspen stands near Grande Prairie from the same time period (~3.8 cm^2/year; Hogg et al. 2002), suggesting that medium and low salinity soils can support healthy, productive aspen.

We found significant differences in basal area growth between sites ($p = 0.036$) with generally faster growth at Child Lake than at Zama Marsh, but there was not a significant site by treatment interaction ($p = 0.15$). Although these data are only for the 1990's, examination of earlier growth rings in these trees showed that the same pattern in basal area growth was evident at Salt Pan Lake and Zama Marsh since the 1960's (data not shown). Growth, and variation in growth, at the high salinity level was similarly small for all sites (Figure 3.1), which could mean that different aspen genotypes are similarly affected by salinity levels that are near the limit of their tolerance, and that intra-specific variation in salt tolerance is low in aspen.

Aspen height-growth rates seemed to be affected by salinity after the juvenile stage of growth (Figure 3.2). Aspen in the highest salinity soils at each site had juvenile height growth similar to aspen in lower salinity soils (Figure 3.2). However, their height growth rate seemed to decrease by age 20 at Salt Pan Lake, and age 36 at Zama Marsh. The trees growing at the high salinity level at Child Lake were still young but their growth rate also seemed to have decreased in recent years (Figure 3.2). Salinity related decreases in growth with age were reflected in site index; the site index of high salinity soils at Salt Pan Lake was 5.1 m lower than the low salinity site index, and at Zama Marsh site index also tended to decrease with increasing salinity (Table 3.1). Research in short term greenhouse and field trials would never observe this pattern because it was only apparent once trees were over 15 years old, and even later in some stands. It is worth noting that the only stand not to display this characteristic growth decline with age, as compared to provincial growth curves, was the low salinity stand at Child Lake – the most productive stand (Figure 3.2; Huang et al. 1994). The fact that salinity affected aspen growth more strongly with time is highly pertinent for oilsands revegetation planning.

If we use site index as an indicator of site productivity, we conclude that saline soils supported a range of aspen productivity. The site index of aspen in the high salinity plots put those stands in a land capability class rating between 4 and 5, conditionally productive or non-productive, while the most productive stand, the low salinity level at Child Lake, was rated at a land capability class of 1 – high capability[2] (Leskiw 2004). Productivity within a site decreased with increasing salinity, but other environmental variables seemed to affect the actual electrical conductivity values associated with declines in growth. The clearest example of this was the difference in productivity between the low salinity soil at Child Lake – high capability, and the high salinity soil at Salt Pan Lake – non-productive; the Child Lake soil was actually more saline than the Salt Pan Lake soil (7.8 dS/m in the lower subsoil at Child Lake and 3.5 dS/m at Salt Pan Lake). It seems as though the lower soil water content of Salt Pan Lake soils (Table 2.2) meant that aspen growth was reduced at lower soil electrical conductivities than at other sites. Soil moisture differences within a site may have contributed to reduced productivity with increasing salinity at Zama Marsh and Child Lake; at those sites the high salinity soils were the highest in elevation and tended to have the lowest soil water content in the topsoil or upper subsoil (Table 2.2, Appendix F).

We measured a variety of parameters related to salinity in three soil depths: electrical conductivity, sodium absorption ratio, soluble chloride, and soluble sulfate, but no parameter related to aspen growth as well as the high, medium, and low designations based on EM-38 readings of the PGM conductivity. Although this result seems somewhat counterintuitive, because the surface soil was where the aspen was rooting, we surmise that the long term salinity level of each plot was closely linked with the PGM salinity. While year to year changes in precipitation, evaporation, and water table level will cause shifts in the salt content of the surface soil, the long term average will probably be dependent on the PGM salinity. Our measurements of conductivity and soluble ions in the surface soil were probably more a snapshot of growing conditions in 2005 or 2006 than a measurement of the long term average.

We must consider possible edge effects on tree growth when discussing the effect of salinity because the soil with the highest level of salinity that aspen can tolerate will always be on the edge of a stand. Harper and Macdonald (2001) described forest edges from lakes in the boreal forest's central mixedwood region and found that the edge had a 40 m wide influence. Stands within the edge had fewer canopy trees and more mid-canopy trees than stands in the forest interior, presumably due to more frequent disturbances at the edge (beaver activity, wind, and flooding). The smaller trees at the saline edges in this study were all canopy trees. The canopy was shorter overall, in contrast to non-saline edges where the canopy was the same height but there were fewer canopy trees. Our observations indicate that beavers were not active in saline wetlands and have not caused disturbance at these sites. Additionally, aspen in the low and medium salinity levels were all within the 40 m zone of edge influence (Appendix F), but medium salinity aspen tended to have higher growth rates than high salinity aspen.

[2] "Land having no significant limitations to supporting productive forestry, or only minor limitations that will be overcome with normal management practices." (Leskiw 2004)

Comparisons to other edges in the boreal forest suggest that salinity effects, not edge effects, were the main cause of reduced tree growth in aspen in our saline study sites

3.3.2. Salinity effects on aspen physiological parameters

3.3.2.1. Foliar nutritional status

The foliar concentrations of nitrogen and phosphorus were mostly normal in all salinity levels. There were significant site by treatment interactions for foliar N and P (Table 3.2), but these were due to very high concentrations of both nutrients in just three trees in the medium salinity plot at Salt Pan Lake (Figure 3.3). Leaves from these trees were very lightweight and turned a dark color quickly after collection. We suggest that a pathogen had infected these trees, causing altered nutrient concentrations in their foliage. These samples were also high in potassium, and low in calcium, manganese, zinc, and aluminum concentrations (Appendix H), but there were no significant treatment effects for these elements. Apart from these outlying samples, all other mean foliar nitrogen concentrations were within the range of foliar nitrogen reported for aspen in northern British Columbia (Chen et. al. 1998), and all mean foliar phosphorus concentrations were within the range reported for aspen in North America (Blinn and Bucker 1989).

Foliar calcium and magnesium concentrations were affected by site but showed no treatment by site interaction (Table 3.2). Calcium concentration was lowest at Zama Marsh and highest at Child Lake. Magnesium concentration was significantly higher at Zama Marsh than at either Child Lake or Salt Pan Lake (Table 3.3). These site differences in foliar nutrients concentrations corresponded to site differences in exchangeable cations (Table 3.4). Zama Marsh had the lowest exchangeable calcium ratio and the lowest foliar calcium. Although the exchangeable calcium ratio was highest at Salt Pan Lake, Salt Pan Lake foliar Ca concentration was not the highest. Total CEC was lowest at Salt Pan Lake (Table 2.3) which may have reduced the availability of Ca in the topsoil, even though the exchangeable calcium ratio was high, and could explain why foliar Ca at Salt Pan Lake was not higher than at the other sites. The higher foliar magnesium in aspen at Zama Marsh compared to Child Lake and Salt Pan Lake closely matched the exchangeable magnesium ratios at those sites (Tables 3.3 and 3.4). Foliar calcium concentrations were all within the range reported for aspen in North America (Blinn and Bucker 1989). A few foliar Mg concentrations, especially at Zama Marsh (Table 3.3, Appendix H) were above the upper limit (3.9 mg/g) for aspen reported by Chen et al. (1998) or Blinn and Bucker (1989); this additional magnesium was probably helpful, not harmful, because excess Mg is generally stored in vacuoles and improves the nutrition of plants (Marschner 1986).

Foliar sulfur concentration was affected by site, treatment, and their interaction (Table 3.2). Aspen foliage contained significantly more sulfur at Zama Marsh than at the other two sites at $\alpha = 0.001$ (Figure 3.3); this result was not surprising considering that Zama Marsh was dominated by sulfur in the soil solution and groundwater and had a high water table (Table 2.2, Figures 2.9 and 3.2). There were also significant differences in foliar sulfur concentration among

the salinity levels at Salt Pan Lake which could be related to small differences in soil solution sulfur (Figure 3.4). The foliar sulfur concentrations at all sites were close to values reported for aspen seedlings in two Alberta plantations (van den Driessche et al. 2003, Liang and Chang 2004).

Neither carbon nor potassium concentrations were affected by treatment or site in this study. A tendency for higher potassium at the medium salinity level at Salt Pan Lake may have been due to a pathogen infection, as described above. Foliar K was within the range reported for aspen in northern B.C. (Chen et. al. 1998).

For micronutrients, there were no significant differences in foliar iron, zinc, or copper concentrations among salinity levels or sites in this study, but manganese and aluminum concentrations were affected by site (Table 3.2). Manganese was higher in foliage from Zama Marsh than from Salt Pan Lake and aluminum was higher in foliage from Zama Marsh and Child Lake than from Salt Pan Lake (Table 3.3). Under saturated soil conditions manganese becomes available as Mn^{2+} (Marschner 1986), so higher foliar Mn at Zama Marsh was probably related to its high water table and frequent saturated conditions. Salt Pan Lake had a deeper water table, never had saturated conditions, and had low foliar Mn. Aluminum availability is tied to pH (Marschner 1986), which may explain why Salt Pan Lake had the lowest foliar Al; Salt Pan Lake soils had only 5-10 cm of mineral soil in the acid range, whereas Zama Marsh and Child lake soils had more than 10 cm of mineral soil in the acid range (Figure 2.3).

Foliar manganese, iron, aluminum, and zinc concentrations measured in these aspen were within the healthy range reported for aspen or plants in general (Marschner 1986, Blinn and Bucker 1989, Chen et al. 1998). Foliar copper concentrations were higher than the range reported by Blinn and Bucker (1989) at every site (Appendix H). For some trees values fell into the critical toxicity level (> 0.2 to 0.3 mg/g; Marschner 1986). Copper tolerance can differ considerably between species (Marschner 1986), and aspen may have a higher critical toxicity level than previously reported because high foliar copper concentration was found in many stands, including the most productive stand at Child Lake. Aspen clones have been shown to have markedly different foliar chemical composition when grown in the same habitat (Lindroth and Hwang 1996), so any significant differences in foliar analyses could be the result of differences in soil properties and other environmental factors among sites, or the result of clonal differences among sites. Also, the fact that we had to collect the second flush of leaves (at Zama Marsh) or partially-eaten leaves (at Salt Pan Lake), because of the forest tent caterpillar defoliation, may have affected our results for foliar nutrients.

The difference between foliar nutrient concentration and nutrient content has been examined in many studies (Timmer and Armstrong 1987, Haase and Rose 1995), and we considered the possible confounding effect of lower foliar nutrients in a treatment that simultaneously resulted in smaller leaves, thus leading to identical leaf concentrations. There were some differences in average leaf weights across sites and treatments (Appendix I), mainly due to three trees with lightweight leaves at the medium salinity level at Salt Pan Lake, two trees with very large leaves at the high salinity level at Zama Marsh, and perhaps to

sampling bias; it was difficult to obtain a representative sample of leaves when each tree had a wide variation in leaf size. We suggest that the effect of foliar content was negligible in this study because we did not experimentally manipulate salinity, so trees have had their lifetime to adjust their growth to soil conditions. Aspen has indeterminate growth and can grow new leaves mid growing season, as we saw after early summer defoliation at Zama Marsh. With greater nutrient availability, the trees are not forced to grow larger leaves because they can grow new leaves. Studies that address nutrient content for aspen generally sample the whole plant (Timmer 1985), which is difficult for mature trees. Clearly for the trees in this study, nutrient content per tree decreased with increasing salinity because, although nutrient concentrations were equal, trees were smaller in higher salinity soils. Since all nutrients were relatively equal among treatments, there was no indication that one or more nutrients were most limiting to aspen growth.

3.3.2.2. Aspen water relations

The negative relationship between growth and salinity in these aspen suggests that roots encountering water stress (due to salinity) signaled the plant to decrease growth in proportion to salinity level (Munns 1993). If salinity caused water deficit and led to stomatal closure we would expect lower internal CO_2 partial pressure (P_{CO2}) in aspen leaves and consequently less discrimination against ^{13}C during photosynthesis (Farquhar et al. 1989). Instead, we found similar foliar $\delta^{13}C$ values for all salinity levels and sites with an average range of -26.3 to -27.1 ‰ (Appendix H), and no significant effects at our pre-determined α (0.001), suggesting that salinity did not affect internal P_{CO2} in these aspen. Tan et al. (2006) also found no effect of severe treatments (compaction and forest floor removal) on aspen foliar $\delta^{13}C$ in north-eastern British Columbia. Foliar $\delta^{13}C$ may be limited as a tool for diagnosing water stress in aspen because aspen is able to make physiological adjustments other than reducing stomatal conductance. By reducing total leaf area in response to higher salinity, aspen could have decreased water requirements (Hart et al. 2000). Alternatively, by decreasing their photosynthetic rate as their stomates closed, aspen internal P_{CO2} could remain constant among treatments. Measuring $\delta^{18}O$ could potentially tease apart these two possibilities (Siegwolf et al. 2001); either way (if there were fewer leaves or each leaf was using less water), it seems that aspen used less water per tree as salinity increased. The potential for trees to share resources such as water, through root grafting (Fraser et al. 2006), common mycorrhizal networks (Simard and Durall 2004), or clonal root connections (DesRochers and Lieffers 2001) could also have affected the water relations of aspen in this study.

Our values for foliar $\delta^{13}C$ are comparable to those reported for regional aspen and hybrid poplar [-26.0 to -27.0 ‰ for young hybrid poplars in a dry year; -27.9 to -28.7 ‰ for a wetter year in the Central Mixedwood (DesRochers et al. 2006); -27.73 ± 0.59 ‰ and -26.22 ± 1.28 ‰ for mature aspen stands in the western boreal (Flanagan et al. 1996)]. It is possible that a drier year would show differences in water stress among the treatments, but we found $\delta^{13}C$ values similar to those in 2006 in preliminary foliar sampling at Child Lake and Salt Pan Lake in a drier year (2004; data not shown). The small range of foliar $\delta^{13}C$ values in

natural aspen stands across the prairie provinces may be an indication that aspen has an optimal P_{CO2} and adjusts physiologically to retain that P_{CO2} in different environments.

3.3.2.3. Nitrogen discrimination in saline aspen stands

Aspen growing in the highest salinity soils were enriched in ^{15}N while the aspen growing in the medium and low salinity soils had similar nitrogen isotope ratios to that of the atmosphere, or were slightly depleted in ^{15}N (Figure 3.5), and this was a significant effect across sites (Table 3.2). Foliar $\delta^{15}N$ was affected by salinity level to a greater degree than any other foliar parameter we measured (Table 3.2). Two unusually high values in the low salinity level at Child Lake were enriched in ^{15}N as much as, or more than, the high salinity trees; these values caused high variation in $\delta^{15}N$ for the low salinity treatment. Otherwise, there was a striking difference in $\delta^{15}N$ between aspen growing in high salinity and in lower salinity, suggesting that there was some difference in ^{15}N discrimination within the soil, between the soil and the aspen, or within the aspen among salinity levels. In preliminary foliar samples (collected midsummer 2004, a drier year than 2006) from Child Lake and Salt Pan Lake, $\delta^{15}N$ values also increased with increasing salinity, but low and medium salinity aspen were more enriched in ^{15}N than in 2006 (Appendix J).

The simplest explanation for these differences in foliar $\delta^{15}N$ is that the source of nitrogen differed in $\delta^{15}N$ among treatments. Soils in the higher salinity plots could have been more enriched in ^{15}N than lower salinity soils. ^{15}N enrichment of plant available nitrogen can occur in systems that are open to N loss (Högberg and Johannisson 1993, Austin and Vitousek 1998) because nitrification and nitrate leaching, ammonia volatilization, and denitrification all discriminate against ^{15}N and leave the remaining soil N enriched in ^{15}N (Högberg 1997). Soils at the high salinity level at each site had the highest mineralizable N (Table 2.3), yet supported the slowest growing trees. If aspen growth was more limited by water deficit than nitrogen as salinity increased, higher N availability may have allowed N loss, causing ^{15}N enrichment of soils and foliage in the high salinity plots. In a drier year, all aspen growth could have been increasingly limited by water, permitting an increase in N loss and ^{15}N enrichment of soil and foliage with increasing salinity; this was the pattern we observed in a drier year (2004; Appendix J).

Other factors could have influenced the foliar $\delta^{15}N$ of these aspen. NO_3^- has lower $\delta^{15}N$ than NH_4^+ (Schulze et al. 1994) so if salinity affected the proportion of NO_3^- versus NH_4^+ uptake, foliar $\delta^{15}N$ could change. Mycorrhizal associations could also account for variation in foliar $\delta^{15}N$ with salinity, since vascular arbuscular (VA) and ectomycorrhizal fungi have been associated with differences in plant ^{15}N enrichment (Michelsen et al. 1998, Schulze et al. 1994) and both can associate with aspen (Allen 1991). Aspen might also discriminate against ^{15}N during uptake, assimilation, or translocation. For example, high osmotic stress can cause N isotope fractionation within a plant (Dawson et al. 2002), and the difference between N supply and N demand can affect ^{15}N

discrimination during N uptake (Yoneyama et al. 1991, Handley et al. 1997, McKee et a. 2002).

Generally these saline aspen stands were more enriched in ^{15}N than aspen in other studies. All or nearly all of the aspen in this study had $\delta^{15}N$ values higher than ranges reported for aspen in interior Alaska (Fry 1991, Kielland et al. 1998) or *Populus tremula* L. in northern Sweden (Michelsen et. al. 1998). Tan et al. (2006) found foliar $\delta^{15}N$ values closer to those in this study; foliar $\delta^{15}N$ was near zero or slightly enriched in ^{15}N for aspen planted on clear-cuts with the forest floor removed in north-eastern British Columbia. These comparisons could imply that these saline aspen stands were more open to nitrogen loss than most aspen stands, causing ^{15}N enrichment of soil and foliage, but without further sampling of ^{15}N in the soil, we can only conclude that there was an interaction between the environmental gradient of salinity (or distance from the forest edge) and the cycling or uptake of nitrogen in aspen stands. This research will add another example to the growing numbers of documented patterns in foliar $\delta^{15}N$ along environmental gradients (e.g. Austin and Vitousek 1998, McKee et al. 2002).

3.3.2.4. Salt ion accumulation

Foliar sodium concentration did not seem to be related to decreases in aspen growth with salinity. Foliar sodium ranged from 0.01 to 0.50 mg/g, for the most part below what has been measured in the second growth of aspen foliage treated with oil sands composite tailings water (0.48 mg/g; Renault et al. 1999), and twice as low as the foliar sodium concentrations in salt-affected mature elm trees (*Elmus americana*, L.) along roadsides in Edmonton, Alberta (Calvo Polanco, personal communication 2007). There was no effect of treatment on foliar sodium, but there was an effect of site (Table 3.2). Sodium was significantly higher at Zama Marsh than at Child Lake or Salt Pan Lake (Table 3.3). Zama Marsh had the highest topsoil exchangeable sodium ratio of the three sites (Table 3.4), which was likely a major factor in the higher foliar sodium. Unexpectedly, large differences in upper and lower subsoil SAR within sites (Figure 2.6) did not seem to affect foliar sodium.

Foliar chloride concentration at the aspen sites ranged from 0.70 to 9.1 mg/g. It was significantly different between sites, and had a significant site by treatment interaction (Table 3.2). Foliar chloride did accumulate to possibly toxic levels (3.5 mg/g; Greenway and Munns 1980) in one aspen stand, the low salinity aspen at Zama Marsh (Figure 3.3), but this did not seem to be related to reduced growth; in fact, those were the tallest trees at Zama Marsh (Table 3.1)! Only at Salt Pan Lake did increased foliar chloride correspond with slower tree growth at the high salinity level (Figure 3.3), but that foliar chloride was below the level shown to cause leaf injury in deciduous trees along roadsides in Edmonton, Alberta (Calvo Polanco, personal communication 2007).

The accumulation of chloride in the low salinity aspen at Zama Marsh seemed linked to the high water table and groundwater chemistry in that plot. Zama Marsh was the only site dominated by SO_4^{2-}, not Cl^-, in the soil and groundwater (Figure 2.9). The relative contribution of Cl^- actually increased as salinity decreased and soil and groundwater Cl^- were highest in the low salinity

plot (Figure 3.4 and Appendix E). Although at Zama Marsh the soil solution Cl^- was still much lower than at Child Lake (Figure 3.4), the combined influence of a high water table (Table 2.2) and moderate chloride concentrations in the groundwater (Appendix E) probably led to high foliar chloride concentrations. At Salt Pan Lake, foliar chloride concentration showed a more intuitive pattern; it decreased from the high to the medium and low salinity levels (Figure 3.3). Higher foliar chloride in the high salinity aspen corresponded with higher upper and lower subsoil solution Cl^- (Figure 3.4). Child Lake soils had the highest soluble Cl^- and steepest gradient in subsoil Cl^- of the three sites (Figure 3.4), but Child Lake trees showed no difference in foliar chloride among treatments (Figure 3.3). It is especially surprising that we did not see higher foliar chloride in Child Lake aspen, or signs of salt-injury, because the high salinity topsoil solution Cl^- was over twice as high as Cl^- in Edmonton roadside topsoils associated with salt-damaged trees (Calvo Polanco, unpublished data), and the upper subsoil solution Cl^- in every plot at Child Lake was above the 25% effect concentration threshold (215-500 mg/L) for woody plants given by Cain et al. (2000). The interactions between groundwater chloride, soil solution chloride, and foliar chloride in these aspen stands were complex and did not seem to be causally linked to reduced tree growth.

Chloride is known to be the most deleterious ion for many plants and the most likely to accumulate in foliar tissues (Greenway and Munns 1980, Shannon et al. 1994), but it did not seem to be strongly related to the slower aspen growth in high salinity soils. It is quite possible that these trees were exhibiting some mechanism of salt tolerance. They may have been excluding both chloride and sodium entirely by selective membrane permeability or by active ion pumping (Allen et al. 1994). They could also have been partitioning the ions within their own tissues to protect the most sensitive tissues, the leaves. Both jack pine and dogwood have shown some ability to restrict ion accumulation to roots and prevent translocation to shoots (Renault et al. 2001, Franklin and Zwiazek 2004); aspen could share this ability. Examining the concentration of sodium and chloride in aspen roots could help elucidate how these trees avoid ion toxicity at these naturally saline sites. Regardless of how ion toxicity is prevented in these aspen, our results support the proposition by Allen et al. (1994) that woody plants that prevent sodium and chloride accumulation in foliar tissues are more able to tolerate saline soil conditions.

3.3.3. Shallow rooting as a mechanism for salt tolerance

One possible mechanism for avoidance of salt stress in trees that has not been explored in previous work is salinity avoidance by very shallow rooting. The majority of other studies on tree salt tolerance have been greenhouse experiments where tree roots are constrained to a small pot, or have occurred where salt was applied to existing tree roots (e.g. along roadsides). Neither scenario permits trees to root in the least saline portions of the soil. Considerable evidence in this study suggests that these aspen were primarily or exclusively rooting in the topsoil, where the electrical conductivity was below 4 dS/m. Foliar nutrients and foliar sodium seemed to be related to exchangeable cation ratios in the topsoil. Very

high subsoil solution chloride and sodium (e.g., especially at Child Lake) did not cause increased foliar chloride and sodium, and only where the chloride rich mean water table level was above 50 cm (at Zama Marsh) did injurious levels of foliar chloride occur. Additionally, aspen grew quickly in height when young – even in high salinity, but height growth slowed earlier with increasing salinity (Figure 3.2). The reduction in growth over time may have been due to restrictions on rooting; aspen ran out of space in the 'favorable' zone so they then reduced their growth and photosynthesis accordingly – which could be why we found no accompanying nutrient deficiency or drought stress symptoms. Perhaps aspen were primarily avoiding the high salts instead of tolerating them. An associated study will directly examine rooting depth to understand how rooting dynamics relate to soil salinity and tree growth.

The depth and quality of rooting space can be two of the most important factors affecting forest productivity; depth of the major rooting zone alone explained 58% of variation in white spruce site index in the Sub-boreal Spruce zone of British Columbia (Wang 1995). Neither water deficit nor ion excess seemed related to reduced aspen growth at the high salinity level in this study, leading to speculation that restricted rooting space may be responsible for growth reductions. If aspen are only able to survive when rooting zone salinity is low, then the rooting zone will be smallest in the high salinity soil and will increase as soil salinity decreases. If aspen growth was in balance with water and nutrient supply, smaller trees would have the same water stress and nutrient concentrations as larger trees, but the nutrients and water used per tree would increase as salinity decreased. The depth of quality rooting material is relatively simple, although possibly expensive, to manipulate on reclaimed landscapes, so it is important to find out more about how rooting depth affects aspen growth in saline soils.

3.4. Conclusions

Productive forests can establish on saline soils, but non-productive forests are also possible. The aspen we studied showed very few signs of water stress, nutrient stress, or ion toxicity when growing on what typical soil analyses would characterize as unfavorable soils. Hydrological characteristics, namely soil water content and water table level, seemed to interact with soil salinity to affect aspen growth. The most productive aspen (the low salinity aspen at Child Lake) did not have a constantly high water table like at Zama Marsh, or a low soil water holding capacity like at Salt Pan Lake, and appeared to be unaffected by moderate salinity in the lower subsoil (7.8 dS/m). Thus it seems that if soil moisture availability and nutrient conditions are favorable, low to moderate salinity in the lower subsoil does not prevent the land from supporting productive forests.

From the measurement of foliar elements and stable isotopes, we cannot deduce if aspen tolerated salinity through slow growth, shallow rooting, internal mechanism(s), or a combination of all three. Soil salinity at all of the sites did seem to be responsible for declines in tree growth rates as trees aged, suggesting that development of rooting limitations over time may be key to aspen growth and survival in saline soils.

Table 3.1. Site index (height [m] at 50 years breast height age) based on the mean for two aspen per high (H), medium (M), and low (L) salinity plot at each site (na = data not available).

	Salinity level		
Site	H	M	L
Child Lake	na	19.5	22.3
Salt Pan Lake	11.5	15.1	16.6
Zama Marsh	12.8	14.4	16.3

Table 3.2. Results of analysis of variance testing for effects of treatment (Trmt = salinity level), site, and interactions between them on the concentrations of sodium, chloride, macronutrients, and micronutrients, and carbon and nitrogen stable isotope ratios in aspen leaves collected midsummer 2006. P values in bold are significant at the pre-defined α (0.001) level.

Variable	Trmt	Site	Trmt×Site
Na	0.30	**<.0001**	0.08
Cl	0.002	**<.0001**	**<.0001**
C	0.65	0.09	0.05
N	**<.0001**	**<.0001**	**<.0001**
P	0.05	0.37	**<.0001**
K	0.01	0.003	0.02
Ca	0.08	**0.001**	0.92
Mg	0.42	**<.0001**	0.58
S	**0.0002**	**<.0001**	**<.0001**
Mn	0.15	**<.0001**	0.02
Fe	0.24	0.74	0.47
Al	0.17	**<.0001**	0.07
Zn	0.95	0.09	0.21
Cu	0.56	0.08	0.17
$\delta^{13}C$	0.12	0.01	0.74
$\delta^{15}N$	**<.0001**	0.03	0.009

Table 3.3. Means (±95% confidence intervals) for foliar elemental concentrations (μg/g dry weight) that had a significant effect of site only. Samples were from 4 trees at each of the high, medium, and low salinity plots at each site. For each element, sites with the same letter were not significantly different at $\alpha = 0.001$.

	Site		
Variable	Child Lake	Salt Pan Lake	Zama Marsh
Ca	16.6[a]	12.6[ab]	10.1[b]
	(2.4)	(3.0)	(1.6)
Mg	3.3[a]	2.9[a]	4.6[b]
	(0.7)	(0.3)	(0.5)
Na	0.16[a]	0.20[a]	0.33[b]
	(0.04)	(0.06)	(0.04)
Mn	0.10[ab]	0.08[a]	0.15[b]
	(0.02)	(0.02)	(0.03)
Al	0.06[b]	0.02[a]	0.06[b]
	(0.01)	(0.01)	(0.01)

Table 3.4. Exchangeable cation ratios for soils at each site; given is the mean ratio for the topsoil of 2 plots at Child Lake and 3 plots at Salt Pan Lake and Zama Marsh.

	Site		
Variable	Child Lake	Salt Pan Lake	Zama Marsh
Ex. Ca^{2+} Ratio	2.40	3.52	0.35
Ex. Mg^{2+} Ratio	0.26	0.11	0.43
Ex. Na^{+} Ratio	0.06	0.01	0.11

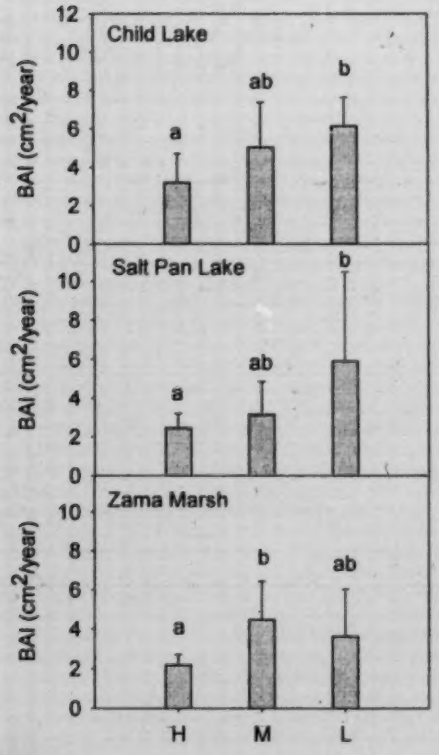

Figure 3.1. Aspen basal area growth rates and 95% confidence intervals at high (H), medium (M), and low (L) salinity plots at each site. Overall basal area growth rate was significantly higher at Child Lake than at Zama Marsh at $\alpha = 0.05$. For each site plots with the same letter were not significantly different at the $\alpha = 0.05$ level.

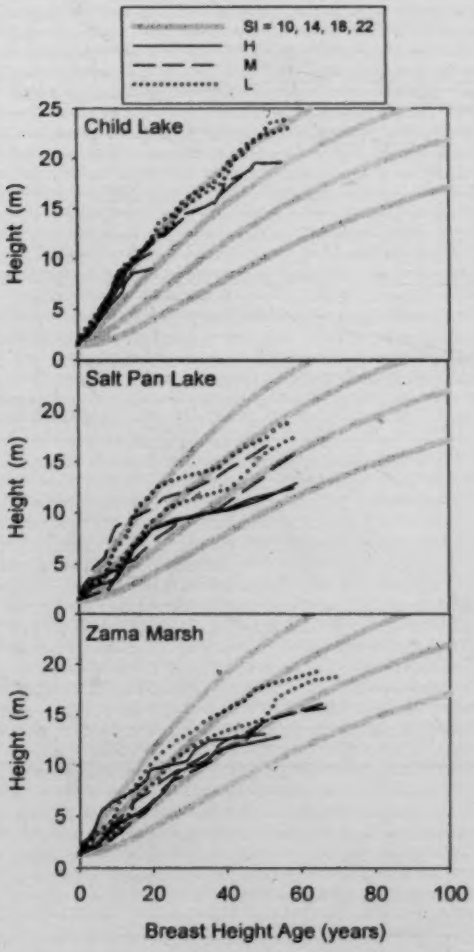

Figure 3.2. Height growth over time for aspen growing in high (H), medium (M), and low (L) salinity plots at each site. Each graph includes separate lines for two trees at each plot and, for comparison, Alberta average growth curves for site index = 10, 14, 18, and 22 (from Huang et al. 1994), a range from non-productive to high capability (Leskiw 2004).

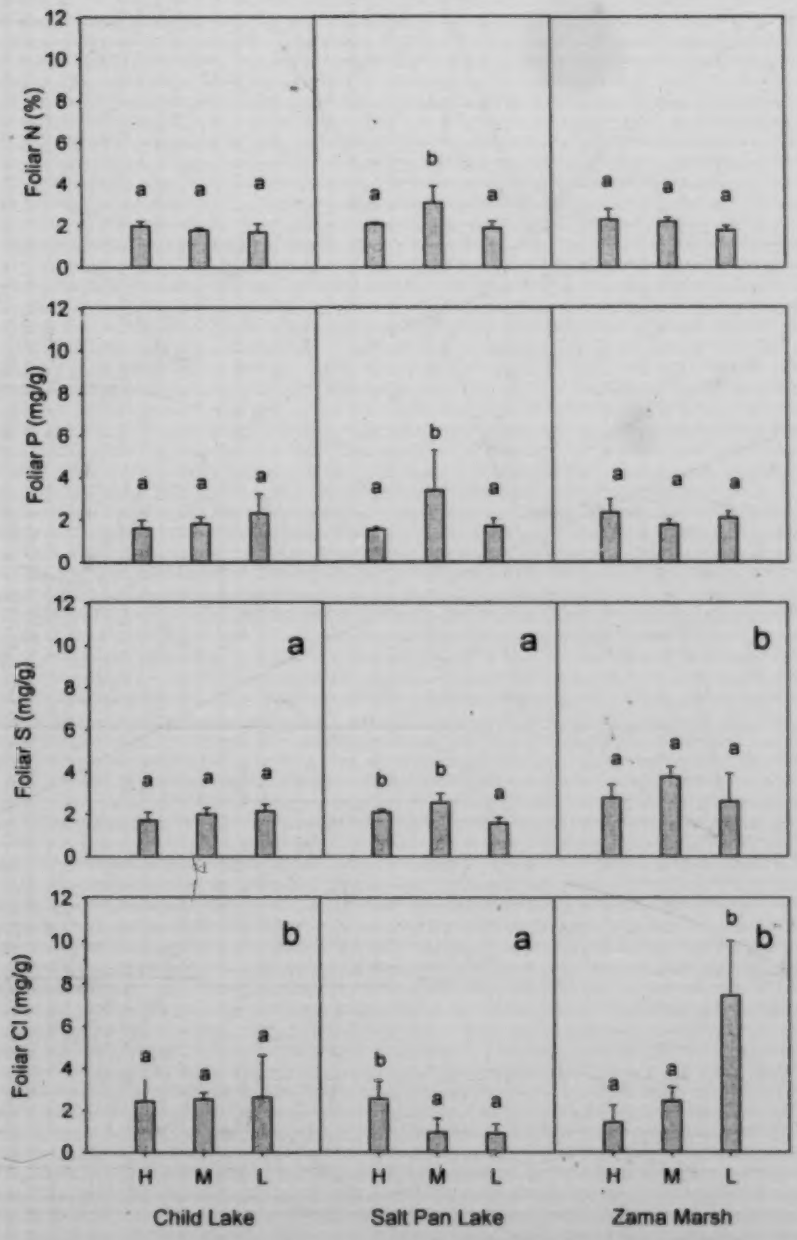

Figure 3.3. Foliar nitrogen, phosphorus, sulfur, and chloride concentrations (mean and 95% confidence interval; foliar parameters affected by trmt×site) in high (H), medium (M), and low (L) salinity plots. For each site, plots with the same letter are not significantly different at the Bonferroni-adjusted alpha level (0.001). For foliar sulfur and chloride, sites with the same letter are not significantly different at $\alpha = 0.001$. Reference line at 3.5 mg/g foliar chloride indicates the lower limit known to cause salinity stress in a variety of plant species (Greenway and Munns 1980). Note - three of four trees at the medium salinity level at Salt Pan Lake may have been affected by a pathogen that caused unusually high foliar N and P.

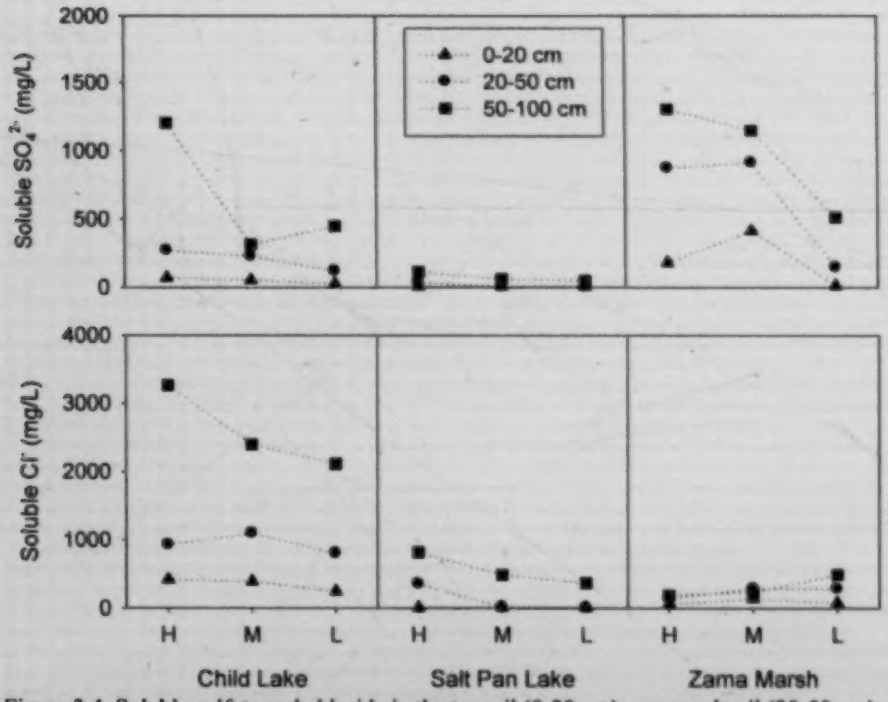

Figure 3.4. Soluble sulfate and chloride in the topsoil (0-20 cm), upper subsoil (20-50 cm), and lower subsoil (50-100 cm) in high (H), medium (M), and low (L) salinity plots under aspen stands at the three sites (symbols are the values for bulked soil samples in each plot weighted by horizon depth).

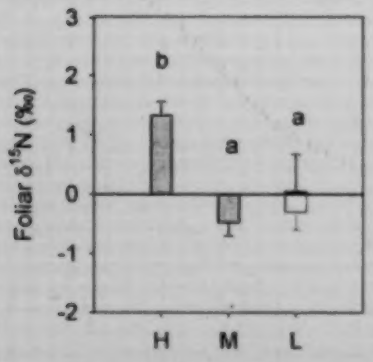

Figure 3.5. Foliar $\delta^{15}N$ (mean and 95% confidence interval; the only foliar parameter significantly affected by treatment only) in high (H), medium (M), and low (L) salinity plots. The empty bar at the low salinity plot excludes two unusually high values from Child Lake. Plots with the same letter were not significantly different at $\alpha = 0.001$.

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Chapter 4. The effects of soil salinity on mature white spruce

4.1. Introduction

White spruce is one of the most important species of the boreal forest, ecologically, and economically. In addition to being sought-after for lumber and pulp, white spruce provides habitat and serves as a food source for a variety of wildlife (e.g., Rusch and Reeder 1978, Mitchell 1952, Greene and Meagher 1998); it also has important effects on understory light (Constable and Lieffers 1996), forest microclimate, and litter (Hannam et al. 2004), thus influencing the understory plant community (Mills and Macdonald 2005, Macdonald and Fenniak 2007). Rural communities in the boreal region depend partially on white spruce for shelter, fuel, and fiber. Worldwide, two of many widespread uses of white spruce and other *Picea* species are for wood products and for landscaping. The prevalence of planted *Picea* spp. along roadsides in many countries has been one reason for study of its apparent sensitivity to deicing road salts (Bogemans et al. 1989, Kayama et al. 2003). In western Canada, research on the effect of salts on *Picea* spp. has been primarily concerned with the reclamation of saline soils in the oilsands region (Renault et al. 1998, 1999, Khasa et al. 2002, Muhsin and Zwiazek 2002, Redfield and Zwiazek 2002, Nguyen et al. 2006).

Some previous work in Canada has found white spruce to have a high sensitivity to salinity. Maynard et al. (1996) found reduced growth of greenhouse-grown white spruce in solutions containing only 92.9 mg/L Na^+, plus CO_3^{2-} (EC = 0.5 dS/m), which is generally considered to be a non-saline solution. The type of salt and the total concentration of salts are two factors affecting white spruce sensitivity to salinity. Fertilizer salts began to affect white spruce growth at higher salinity (EC = 3.0 dS/m) than did $NaCO_3$ (Phillion and Bunting 1983, Maynard et al. 1996). Compared to other plants, white spruce has often demonstrated lower salinity tolerance; McKenzie et al. (1993) compared the salinity tolerance of 28 tree and shrub species in a field trial in southern Alberta and found white spruce to be the 4th most sensitive species.

Although many studies have concluded that white spruce and other *Picea* species are salt-sensitive, other studies have been contradictory. For example, greenhouse-grown white spruce had the second highest survival rate under salinity treatments, second only to one jack pine seed lot, and higher than alder (*Alnus rubra* Bong.), aspen, lodgepole pine, and four other jack pine seed lots (Khasa et al. 2002). Renault et al. (1998) found that some individual greenhouse-grown white spruce seedlings showed remarkable salt tolerance, even to a 6.55 dS/m hydroponic solution. Evidence of some degree of salt tolerance in *Picea* spp. has come from field observations as well. After a brine spill in Swan Hills, Alberta, black spruce showed some ability to avoid Cl^- accumulation in needles (Edwards and Blauel 1975). At another brine spill, white spruce accumulated Cl^- in needles, but seemed to exclude Na^+ (Rowell and Crepin 1977). White spruce seedlings were found to successfully germinate on salt affected flood plains in

interior Alaska, even though establishment was low; in that case it was likely that frequent flooding and siltation, rather than salinity, killed germinants (Viereck et al. 1993). Clearly, more research is required to understand how salinity affects white spruce, and whether the species could be a component of revegetation on saline soils.

A plant's reaction to a stressful environment (such as soil salinity) integrates many physiological components and this has been illustrated successfully in many studies through the use of natural abundances of carbon and nitrogen stable isotopes, as introduced in Chapter 3. Stable isotopes have been used to indicate the effect of water stress, nitrogen stress, and nutrient changes on photosynthesis and nitrogen assimilation in white and black spruce seedlings (Patterson et al. 1997, Livingston et al. 1999, Pritchard and Guy 2005). Foliar nutrient concentrations can also be a helpful tool in diagnosing plant stress. Critical nutrient concentrations, optimum nutrient ratios, and vector analysis have been used successfully on many conifer species to diagnose nutrient deficiencies or toxicities (Timmer 1991). Foliar sodium and chloride concentrations can be another diagnostic tool; previous research on *Picea* spp. along salt-affected roadsides has established that a tree's health declines when salt ions accumulate in needles (Kayama et al. 2003, Bogemans et al. 1989). Thus, foliar elemental concentrations and stable isotope ratios could help identify and quantify white spruce physiological stress in saline soils.

White spruce is one of the most dominant native species in the boreal forest, including northeastern Alberta (Rowe 1972), so ensuring that it can be established on reclaimed oilsand landscapes is critical for meeting land capability and biodiversity regulations in Alberta (TERRE Workshop 1998). A portion of the reclaimed landscape is expected to be affected by salinity; therefore, understanding how salts affect the survival and growth of *Picea* spp. will help ensure that reclamation procedures create soil conditions that can support stands of white spruce. We sampled mature stands of white spruce along natural gradients of soil salinity to examine the long-term effects of salinity on white spruce growth and physiology. The information from this study will add to the knowledge gained about aspen in Chapter 3 to help us understand how future forests might develop on salt-affected soils in the oilsands region.

The objectives of this study were (*i*) to examine the relationship between white spruce growth and soil salinity; (*ii*) to understand whether salinity caused water stress in white spruce; (*iii*) to investigate whether salinity affected nutritional status or nitrogen uptake in white spruce; and (*iv*) to explore the relationship between salinity and salt ion accumulation in white spruce foliage. The influences of environmental factors besides salinity on white spruce growth and physiology were also investigated.

4.2. Methods

4.2.1. Site description and plot set-up along the salinity gradient

The sampling for this study was conducted at naturally saline sites in northern Alberta with forests dominated by white spruce: Benchmark, Clearwater, and Salt Plains (Table 2.1, Figure 2.1). At each site there was a distinct boundary between forest vegetation and vegetation dominated by grasses and shrubs. This boundary corresponded with a decrease in the electrical conductivity of the topsoil from above 4 dS/m (grass and shrub vegetation) to below 4 dS/m (forest vegetation; Figure 2.4). We located a transect of decreasing salinity from the forest edge to the forest interior at each site and identified appropriate locations for 5×20 m^2 sampling plots at high, medium, and low salinity levels (Figure 2.2). High, medium, and low salinity plots were based on relative differences in the conductance of the parent geological material within each site, measured with an EM-38 (Geonics Ltd., Mississauga, Ont., Canada). At each site the high salinity plot was located adjacent to the forest edge (the limit of salinity tolerance for trees at each site) and the low salinity plot was located where the least saline soils were found at the site. Salinity varied with depth in the soil profile at each site and the levels of salinity varied among sites. As such the 'high', 'medium', and 'low' levels of salinity were only relative to each other within a site and not between sites. We hereafter refer to the three locations along the salinity gradient at each site simply as 'high', 'medium', and 'low' because there was no single quantitative measure of salinity in any plot. The electrical conductivity (EC) throughout the soil profile was measured once in each plot, generally confirming that soil salinity decreased from the high to the low salinity plots, and that the absolute EC differed among sites (Figure 2.5).

Each site had saline soils, but many other soil characteristics differed among sites. Soils at Benchmark were Gleyed Gray Solodized Solonetzes, Gray Solodized Solonetzes, and Gray Solods, in the high, medium, and low salinity plots, respectively. Along the entire salinity gradient soils at Clearwater were Lignic Folisols and soils at Salt Plains were Humic Regosols (Figure 2.3; Soil Classification Working Group 1998). The understory vascular plant community at each site was typical of white spruce forests in northern Alberta.

4.2.2. Tree sampling

Four trees per salinity level were selected for sampling using a stratified random sampling method. Trees were stratified by canopy dominance and health; candidate trees were dominant canopy trees not overtopped by a neighboring stem, free from disease, damage, or rot, and safe to fell. Two trees that met these criteria were randomly selected to be felled for stem analysis and two additional trees were cored twice with an increment borer at 1.3 m in height for tree ring analysis. The diameter and height were measured on all trees in each 100 m^2 plot. A few of the felled trees were located just outside of the 5×20 m area where we performed soil sampling and stand measurement. Salt Plains was in a special preservation management zone of a National Park, so we were unable to fell trees. Instead we cored four trees per plot.

During tree felling, stems were cut somewhere between 0.3 m (stump height) and 1.3 m (breast height). After felling, stem length was measured and stem cross-section samples (tree cookies) were cut and collected at 1.3 m, 2.3 m, 3.3 m, and every meter thereafter until the top. A cookie was also cut and collected at stump height (0.3 m). Tree cookies were oven dried at 65 °C and the diameter at 1.3 m was remeasured to adjust future calculations for shrinkage. Diameters decreased 6% during oven drying. Tree cores were air dried and mounted onto wooden blocks. All samples were then sanded with progressively finer grades of sandpaper until tree rings could be clearly seen.

A dissecting microscope was used to count tree rings and cross date all samples within a site (Yamaguchi 1991). Each sample was dated along 2 radii to ensure correct ring counting.

4.2.3. Ring width measurement

Ring widths were measured on the breast height samples – two cookies and two cores per salinity level per site. A Velmex microscope-sliding stage system (Velmex Inc., Bloomfield, NY, USA) was used to measure tree ring widths. The inner and outer radius of each ring was measured on two average radii per sample to increase the accuracy of ring width measurement and used to calculate the area of wood in each ring, or the basal area increment (BAI) using the equation:

$$BAI = \pi(R^2_n - R^2_{n-1})$$

where R is the tree radius and n is the year (Kolb and McCormick 1993, Hogg et al. 2002). Tree ring widths decrease with tree age because circumference increases; calculating the BAI is one way to account for that change, enabling comparison of growth rates in trees of different ages. BAI is expressed as area before drying. The ends of many cores broke near the bark and the more recent rings were lost or jumbled, so there was not a full sample set for the 1990's for white spruce. In the 1980's and 70's, there were many years with poor growth, so the 1960's were used as the best decade for comparisons among trees of differing ages. The 1960's included years of poor, medium, and good growth similar to the 1990's. The mean BAI for 1960-69 inclusive for each tree was used in subsequent analyses.

Basal area growth data were analyzed with ANOVA using the following model:

$$Y_{ijk} = \mu + Site_i + Treatment_j + Treatment \times Site_{ij} + e_{k(ij)}$$

where Y_{ijk} is the k^{th} tree in the j^{th} site of the i^{th} salinity level, which is equal to the overall mean (μ), plus the effect of the i^{th} site (Benchmark, Clearwater, or Salt Plains), the j^{th} treatment (high, medium, or low salinity), the interaction of the i^{th} site and the j^{th} treatment, and the random error among trees within a treatment at a site ($e_{k(ij)}$). Both 'Site' and 'Treatment' were considered fixed effects. The general linear model procedure in the SAS software package (v 9.1; SAS Institute Inc.,

Cary, NC, USA) was used to analyze the data. The assumptions of homogeneity of variance were not met with these data, even after square-root (and logarithmic) transformation, so the heterogeneous variances were taken into account in the model using the mixed procedure in SAS Version 9.1 (SAS Institute Inc.); the untransformed data are presented in this chapter. When there were significant effects in the model at $\alpha = 0.05$, least squared means were compared with a comparison-wise $\alpha = 0.05$.

4.2.4. Stem analysis

After cross-dating, the age and height in the tree were recorded for each tree cookie. The age at breast height (BH age) was used because of the difficulty in obtaining the absolute age in the boreal forest (Gutsell and Johnson 2002, Peters et al. 2002). To account for the problem in stem analysis of underestimating the actual tree height at a given age, we adjusted the data with Carmean's (1972) algorithm for each tree separately (Dyer and Bailey 1987, Wang 1995). These data were plotted to create age-height growth curves for each tree. Clearwater data were compared visually to provincial average growth curves (Huang et al. 1994), but Benchmark and Salt Plains data were compared to Northern Mixedwood growth curves, as recommended by Wang and Huang (2000). Two trees at Clearwater had long periods of time with no height growth, likely because lightning damaged their top and it took many years for a new leader to gain dominance. Only the portions of their curves before this gap in height growth occurred were included in Figure 4.2. Site index (height [m] at 50 years BH age) was calculated from growth curves using the equation for a straight line between the age-height points on either side of 50 years old; the mean site index for the two trees in each plot was reported. A SAS program published by Huang et al. (1994) with parameters from Wang and Huang (2000) for the Northern Mixedwood natural region was used to estimate the site index for trees at Salt Plains. The total height and BH age were the inputs into the model; the mean site index for 4 trees per plot was reported. No statistical analysis was performed on stem analysis data because of the small sample size (2 trees per plot). When tree cores were taken through or next to the pith, allowing accurate aging of additional trees, these age-height points were added to Figure 4.2.

4.2.5. Foliage sampling and analysis

White spruce needles were collected from four trees in each plot in the summer of 2006. Foliage was sparse or lacking on the lower part of the crown at Salt Plains (where trees could not be felled, and a shotgun could not be used to fell foliage because the site was in a National Park), so only 2 trees were sampled in the high and medium salinity plots, and 3 trees were sampled in the low salinity plot. For the felled trees at Benchmark and Clearwater, the foliage was collected from the top third of the crown. For all other trees, foliage was collected, using a pruning pole, from as high as possible in the crown. We collected at least 500 needles from each tree from the current year and the previous 2 years of growth and pooled them. Needles were air dried and 500 needles were counted for each

tree. All needles were then oven dried at 65 °C, weighed, and finely ground with an electronic ball grinder.

The concentrations of Na, macronutrients (P, K, Ca, Mg, and S), and micronutrients (Mn, Fe, Al, Zn, and Cu) were determined by the Analytical Services Laboratory at the Northern Forestry Centre in Edmonton, Alberta. Samples were digested with a CEM (Matthews, NC, USA) MARS Xpress microwave digestion system and then measured on a Spectro (Kleve, Germany) Cirrus Inductively Coupled Plasma Atomic Emission Spectrophotometer. Extractable foliar Cl concentration was determined by ion chromatography (DI 300; Dionex Corporation, Sunnyvale, CA, USA) on a filtered water sample obtained by combining two successive 1-hr extractions of 0.05 g samples with boiling water (Franklin and Zwiazek 2004). Foliar C and N concentrations were determined by the Dumas combustion method on a Carlo Erba (*now* CE Elantech Inc., Lakewood, NJ, USA) NA1500 Elemental Analyzer (Carter 1993). All foliar elemental concentrations were expressed on a dry weight basis, and were compared to previously-published values for white spruce and other closely related species. Relationships between needle weight, N content, and N concentration were explored graphically using a vector analysis approach (Haase and Rose 1995).

$\delta^{13}C$ and $\delta^{15}N$ were determined using a Finnigan Delta Plus Advantage isotopic ratio mass spectrometer with a ConFlo III universal interface (Thermoquest, Bremen, Germany). A Costech (Valencia, CA, USA) ECS 4010 elemental analyzer was used as a peripheral to combust the samples according to the Dumas method (Carter 1993). Stable isotope composition is expressed as a ratio relative to Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen according to the equation:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = 1000 \times (R_{sample}/R_{standard} - 1)$$

where R is the abundance ratio of the heavier isotope to the lighter isotope (Dawson et al. 2002).

Data for each variable measured on the foliar samples were analyzed with ANOVA using the same general linear model as for the basal area increment data. All variables with a significant effect met the homogeneity of variance and normality assumptions of ANOVA. Forty-eight comparisons were made (3 tests for 16 variables) on the foliar samples; to retain an experiment-wide alpha of 0.05, we made a Bonferroni adjustment and differences were only considered significant at the alpha = 0.001 level. This adjustment in alpha also improved the likelihood that statistically significant results were also biologically meaningful. When a significant effect of site, treatment, or a site by treatment interaction was found, the least squared means for the appropriate effect were also compared at alpha = 0.001.

4.2.6. Soil sampling and analysis

Soils were sampled in 2005 (Salt Plains and aspen dominated sites) or 2006 (Benchmark and Clearwater). In each plot we dug three soil pits: one central

soil pit, and pits between the center and each plot end (Figure 2.2). We sampled the soil by horizon and bulked the corresponding soil samples from each pit into one sample per horizon for each plot. In the laboratory, all samples were air dried and ground to pass through a 2 mm sieve. Soluble Cl^-, Na^+, Mg^{2+}, and Ca^{2+} concentrations were measured on saturation extracts (Sparks 1996) by ion chromatography (Cl^-) with a DX600 (Dionex Corp., Sunnydale, CA, USA) and atomic absorption spectroscopy (Na^+, Mg^{2+}, and Ca^{2+}) with a SpectrAA 880 (Varian Inc., Mississauga, Ont., Canada). In order to make comparisons among sites that had different horizons we calculated weighted Cl^- concentrations and sodium absorption ratios ($SAR = [Na^+]/\sqrt{([Ca^{2+}]+[Mg^{2+}])}$) by depth for three depths: topsoil (0-20 cm), upper subsoil (20-50 cm) and lower subsoil (50-100 cm). Linear regression (SAS Version 9.1, SAS Institute Inc.) was used to examine the relationship between salt ions in the topsoil and salt ions in the forest floor for the aspen and white spruce dominated sites. We have no data on within plot variation for soil properties because we bulked soil into one sample per horizon per plot.

4.3. Results and discussion

4.3.1. The effects of salinity on white spruce growth

There were no differences in basal area growth among the salinity levels ($p = 0.46$) and the salinity level by site interaction was not significant ($p = 0.31$). The only significant effect was among sites ($p = 0.004$), with higher basal area growth at Clearwater than at Benchmark or Salt Plains (Figure 4.1). We found high variation in basal area growth among trees within plots, especially at Clearwater. Surprisingly, at Clearwater and Salt Plains, the individual tree with the fastest 1960's basal area growth (13.9 and 6.8 cm^2/year, respectively) was growing at the high salinity level, and at Benchmark the second fastest growing tree (5.6 cm^2/year) was at the high salinity level. Although these data only compare basal area growth in the 1960's, examination of earlier and later annual rings in these trees showed the same trend – growth rates were similar among treatments and some of the fastest growing trees were found at the high salinity level (data not shown).

White spruce height growth was similar among salinity levels at Benchmark and Salt Plains, but tended to increase with decreasing salinity at Clearwater (Figure 4.2). Most trees at Benchmark had a different pattern in height growth over time than other white spruce in the Northern Mixedwood (Wang and Huang 2000); their growth slowed in comparison with the expected growth rate when they were ~ 50 years BH age, indicating a possible increase in growth limitation(s) with stand age. Trees at Salt Plains had slower height growth rates than trees at Benchmark, with a site index of 5.6 - 7.0 m compared to 12.1 - 12.8 m for Benchmark (Table 4.1). Stand age seemed to differ among salinity levels at Salt Plains, but although trees were older at medium salinity than at low or high salinity levels, they all seemed to span the same range of site indexes (Figure 4.2).

There was greater variation in height growth among treatments at Clearwater than at the other sites (Figure 4.2). The general trend of increasing site index with decreasing salinity at this site (Table 4.1) did not hold true for all trees, with one low salinity tree growing at the same slow rate as the high salinity trees (Figure 4.2). In contrast to the other sites, the height growth over time of white spruce at Clearwater followed the same pattern as those in the province-wide data set, and two trees were following the growth curve for a site index of 16 or higher (Figure 4.2).

White spruce growth did not decline with increasing salinity, even though the forest floor of the high salinity plots at Clearwater and Salt Plains had an EC higher than 0.5 dS/m, which was the lower limit found to reduce white spruce growth in a greenhouse study by Maynard et al. (1996). McKenzie et al. (1993) estimated that white spruce growth was reduced by 12.7% for each dS/m increase, yet we found no reduction in growth of mature trees between plots that had a difference of over 7 dS/m in the upper subsoil and a difference of 1.7 to 3.1 dS/m in the topsoil.

Although it is encouraging that white spruce can establish forest stands on soils previously thought to be too saline, forest productivity at these sites was low. Clearwater was the only site at which trees were growing fast enough to achieve a land capability rating above 4 – Conditionally Productive, while most of the sampled white spruce stands would be rated at 5 – Non-Productive (Leskiw 2004). Where trees at Clearwater were growing well enough to be rated at 2 or 1 – Medium or High Capability (Site Index > 18), the soil was essentially non-saline to 100 cm depth (Figure 2.5). Whereas some high growth rates were achieved in the low salinity plot at Clearwater, tree growth in the low salinity plots at Benchmark and Salt Plains was lower than we would have expected based on their medium-rich to rich nutrient regimes and the subhygric to mesic moisture regimes. It could be that the capacity of white spruce to grow slowly was precisely how it tolerated these unfavorable soils. Khasa et al. (2002) found white spruce to be the slowest growing species, but also one of the species with the highest survival rate, in a comparative salinity experiment. Unfortunately, slow growth as a mechanism for salt tolerance is not a desirable trait for most saline soil management considerations.

4.3.2. The effects of salinity on white spruce physiological parameters

4.3.2.1. Foliar nutritional status

Nearly all of the white spruce were severely to very severely deficient in nitrogen (< 1.55 %), slightly to moderately deficient in phosphorus (< 1.6 mg/g), and possibly deficient in sulfur (< 1.2 mg/g), according to levels proposed by Ballard and Carter (1985), although all trees had a N:P ratio < 12.5, and a N:S ratio < 13.6 suggesting that N was more deficient than P or S. Ballard and Carter's (1985) standards for white spruce are based on seedling nutrition and have been criticized as being too high for nitrogen and too low for phosphorus, potassium, and calcium for mature trees (Wang and Klinka 1997). However, comparisons with studies of mature white spruce also suggest that most trees, especially at Benchmark, were somewhat deficient in nitrogen. The white spruce

in this study were at the low end of the foliar N range reported for the sub-boreal spruce region of British Columbia (0.82 – 1.43%), and 75% of trees at Benchmark were below that range (Wang and Klinka 1997). Benchmark foliar nitrogen values were close to those (0.7%) associated with needle yellowing in interior Alaska (Schulze et al. 1994).

Compared to other mature white spruce, most foliar P, K, Ca, Mg, and S concentrations appeared to be normal or high. Mean foliar potassium and sulfur concentrations, nearly all mean foliar magnesium concentrations, and most mean foliar phosphorus concentrations in this study were within the range reported for the sub-boreal spruce region of B.C. (Appendix K, Wang and Klinka 1997). Most foliar calcium concentrations were higher than the highest value reported (8.7 mg/g) for mature white spruce in B.C. or in North America (Wang and Klinka 1997, Blinn and Bucker 1989). Calcium is non-toxic, even in high concentrations, and plants can have up to 50 mg/g Ca in their tissues, (Marschner 1986) so unusually high foliar calcium in saline stands of white spruce was probably not harmful.

Iron was possibly deficient in white spruce at Benchmark and Clearwater (< 0.050 mg/g); all other foliar micronutrients were adequate (Appendix K, Ballard and Carter 1985). Aluminum and copper were the only micronutrients that were higher in some trees than mean values reported for mature white spruce in North America (Blinn and Bucker 1989). One tree at Salt Plains and one tree at Benchmark had foliar Cu above the critical toxicity level for crop plants (> 0.020 - 0.030 mg/g) but copper tolerance can differ greatly among species (Marschner 1986) so it is difficult to say whether these levels were harmful. Only one study could be found that provided values for comparison of foliar aluminum: the foliar aluminum for most trees in this study was between values found for white spruce seedlings in control (0.018 mg/g) and severe site-preparation (0.106 mg/g) treatments in Alberta plantations (Macdonald et al. 1998). It is possible that high foliar aluminum had a negative effect on white spruce in some of these naturally saline stands, which was unexpected because high aluminum is usually a problem only in acidic soils (Marschner 1986).

No macronutrients were significantly affected by the different levels of soil salinity or by site×treatment interactions (Table 4.2). The only difference in foliar macronutrients among sites was for foliar nitrogen (Table 4.2). Foliar nitrogen concentration was significantly lower at Benchmark than at Clearwater or Salt Plains (Table 4.3). Low foliar N at Benchmark corresponded with low soil N; Benchmark had the lowest total and mineralizable nitrogen concentrations of the three sites (Table 2.3). Likewise, white spruce needles at Benchmark were low in N content and concentration compared to the other sites (Figure 4.3), so low foliar N concentrations were not a result of dilution (Haase and Rose 1995). Foliar elemental concentrations can be difficult to interpret if needle weights are changing simultaneously (Timmer 1991), but this is of minimal concern to our results because we did not apply a 'treatment' *per se* and these trees have had their lifetime to adjust growth and foliage quantity to their environmental conditions; moreover, needle weights were very similar among sites and treatments (Appendix L).

There were no significant effects of treatment or site×treatment interactions on foliar micronutrients, but there was an effect of site on foliar manganese and iron (Table 4.2). Manganese was higher in trees from Benchmark than from Clearwater and iron was higher in trees from Salt Plains than from Benchmark or Clearwater (Table 4.3). Iron solubility can be low in aerated alkaline soils, causing iron deficiency in many plants, but when alkalinity occurs in conjunction with high organic matter, hydroxamate siderophores can substantially increase iron solubility (Marschner 1986). These compounds are mainly produced by soil fungi with a high affinity for Fe^{3+} at high pH (Marschner 1986). Another source of soluble iron in soils with organic matter and pH > 8.5 is sodium humates, formed when $NaCO_3$ disperses organic matter and complexes with iron and magnesium (Marschner 1986). These two sources of soluble iron were both likely at Salt Plains where both soil pH and organic matter content were high, which would explain high foliar Fe. Lower foliar Fe concentrations were measured for Clearwater and Benchmark which had pH > 8.5, or high organic matter, but not both. However, sodium humates can also increase manganese solubility, and foliar Mn was highest at Benchmark not Salt Plains. High foliar Mn is associated with iron deficiency; dicot roots deficient in iron can pump H^+ and phenolic compounds into the soil, lowering soil pH and increasing Fe and Mn solubility (Marschner 1986). Higher foliar Mn at Benchmark could be the result of this process if Fe was quite deficient at Benchmark. Increased Al solubility leading to high foliar Al could also be a negative side effect of roots lowering the rhizosphere pH to increase Fe solubility (Marshner 1986), which could explain high foliar Al at Benchmark, but not at the medium and low salinity level at Salt Plains, where Fe was adequate. Most micronutrient research has been on agricultural species, so further examination of Mn, Fe, and Al nutrition of trees in alkaline soils could be helpful for ensuring that reclaimed alkaline soils are nutritionally adequate.

4.3.2.2. White spruce water relations

Foliar $\delta^{13}C$ values were similar among sites and treatments (Table 4.2), suggesting that measured differences in soil salinity did not affect white spruce via water stress. Alternatively, it is also possible that white spruce experiencing water stress decreased stomatal conductance and photosynthesis simultaneously so that their internal P_{CO2} remained unchanged (Farquhar et al. 1989). The mean values of foliar $\delta^{13}C$ for each plot fell between -25.9 and -26.6 ‰ (Appendix K), which is higher (less negative) than for white spruce seedlings, including those that were water-stressed (Patterson et al. 1997, Livingston et al. 1999, Tan et al. 2006). It is difficult to compare foliar $\delta^{13}C$ values between seedlings and mature trees. However, our results might suggest that the white spruce trees we sampled on these saline sites discriminated less against ^{13}C during photosynthesis, presumably because of a lower internal CO_2 partial pressure due to stomatal closure.

4.3.2.3. Nitrogen discrimination in saline white spruce stands

Although there was a strong suggestion of a site×treatment interaction on foliar $\delta^{15}N$ ($p=0.01$), it was not significant at our predetermined α (0.001), and neither were the effects of site or treatment separately (Table 4.2). At Benchmark, the site with the lowest nitrogen in the soil and foliage, low salinity trees tended to be more enriched in ^{15}N than high and medium salinity trees (Appendix K). Differences in foliar $\delta^{15}N$ could be caused by N-sources with differing amounts of ^{15}N, or by ^{15}N discrimination by trees during N uptake and assimilation (Högberg 1997). White spruce in these saline stands had foliar $\delta^{15}N$ values similar to those reported in other studies and the high variation found in this study, especially at Salt Plains (Appendix K) was not unusual. Foliar $\delta^{15}N$ for trees in this study varied from +0.3 to -3.6 ‰, a narrower range than for white spruce at the northern treeline of Alaska (-0.64 to -11.16 ‰; Schulze et al. 1994). Other values reported for Alaskan white spruce seedlings and mature trees in unburned areas had narrower ranges: -3.27 to -8.46 ‰ (Fry 1991) and ~ -1.7 to -4.5 (Kielland et al. 1998), but no positive values.

4.3.2.4. Salt ion accumulation

Neither treatment nor site differences affected the foliar sodium concentration of white spruce in this study (Table 4.2), even though the SAR in the soil differed substantially among salinity levels (Figure 2.6). Most trees had foliar sodium concentrations under 0.3 mg/g (Appendix K), which is an order of magnitude less than the shoot sodium found in white spruce seedlings grown in 25 mM NaCl with and without mycorrhizae (Nguyen et al. 2006). The foliar sodium concentration in the trees we sampled was at the level of control seedlings in a greenhouse study (0.2 mg/g), and far below seedlings grown in oilsand composite tailings water (8.5 mg/g) (Renault et al. 1999). Compared to mature white spruce foliage along salt affected roadsides in Edmonton, Alberta, most trees in this study had foliage closer to non-salt-affected than salt-affected tree foliage (Calvo Polanco, personal communication 2007). There were a few outliers for foliar sodium concentration in this study, most notably one tree at the medium salinity level at Clearwater with 1.9 mg/g foliar sodium, an order of magnitude above the foliar sodium for most other trees at that site. This was above the level associated with foliar injury in roadside white spruce in Edmonton (Calvo Polanco, personal communication 2007). This high level of foliar sodium did not seem to be related to reduced tree growth or discolored needles, but it did correspond with higher than average foliar chloride.

Most of the foliar chloride concentrations in this study were less than 0.3 mg/g (Appendix K) and far below 3.5 mg/g, which is considered to be the lower limit for salt stress in many species (Greenway and Munns 1980). Foliar Cl concentrations in this study were also below 1.8 mg/g Cl, the level associated with injury to needles of white and black spruce after a brine spill (Rowell and Crepin 1977) and with photosynthesis decline in two spruce species from Japan (Kayama et al. 2003). Likewise, our measured foliar Cl concentrations were below those found in both control and salt affected roadside white spruce in Edmonton (Calvo Polanco unpublished data). The soil solution Cl^- in the high

salinity upper subsoil at every site, and even in the high salinity topsoil at Clearwater and Salt Plains, was above the 25% effect concentration threshold for woody plants (215-500 mg/L; Cain et al. 2000; Figure 4.4). These high amounts of chloride in the soil seemed to have no effect on the chloride in needles ≤ 3 year old.

Although we did not see foliar Na or Cl ion accumulation in white spruce at any salinity level, this result could have been a function of our sampling methods. Sodium and chloride concentrations have been shown to increase in spruce needles over time and to decrease needle life span (Kayama et al. 2003). Since we only collected foliage that was ≤ 3 years old, we might have missed needles with injurious concentrations of salt ions. Early death of needles with high salts could explain why many trees at the Salt Plains had sparse foliage, but the old age of those trees is another important factor. Regarding the one tree at Clearwater that did have injurious levels of foliar Na, it is possible that a sampling mistake occurred on that tree and older, more salt affected, needles were collected. Even if white spruce did accumulate salt ions in its older foliage, the apparent exclusion of sodium and chloride from its younger needles was probably an important factor allowing white spruce to survive at these saline sites (Allen et al. 1994). Investigation into the concentration of salt ions in older foliage and in roots at these sites could elucidate whether mature white spruce do exhibit some mechanism(s) for salt tolerance, or if they predominantly avoid salts. Roots could act to restrict upwards salt transport within the tree, as found in laboratory experiments with white spruce seedlings (Muhsin and Zwiazek 2002), or other tissues could compartmentalize ions in vacuoles (Jacoby 1999) to protect the youngest foliage, the tissues with the highest photosynthetic capacity (Brooks et al. 1996, Greenway et al. 1992).

Regression analysis between sodium and chloride concentrations in the topsoil and the forest floor across all white spruce and aspen sites showed that salts in the forest floor were related to salts in the mineral soil (Figure 4.5). The sodium absorption ratio of the topsoil, which is a good indication of the availability of sodium in relationship to other cations, was significantly related to the soluble sodium of the forest floor ($p < 0.0001$, $R^2 = 0.87$). Soluble chloride in the topsoil and forest floor were also significantly related to one another, both with and without the outlier ($p < 0.004$, $R^2 = 0.44$, without the outlier). Salts could have moved from the mineral soil to the forest floor through capillary rise, but we suggest that this is unlikely because the presence of a forest floor was found to nearly eliminate capillary rise on salt-affected floodplains in Alaska (Dryness and Van Cleve 1993). Instead, we propose that Na^+ and Cl^- in the forest floor were caused by the cycling of Na^+ and Cl^- by plants; Na^+ and Cl^- were absorbed into plant tissues in relation to their supply and then returned to the soil as litterfall or through fine root turnover. Both vascular and non-vascular plants could have contributed to this salt ion cycling.

Salt accumulation in litter has been found for *Tamarix* spp. in the western USA, and is problematic because it increases the salinity of the surface soils, preventing the establishment of other species (Ladenburger et al. 2006). To our knowledge, cycling of salt through vegetation has never been documented in the

boreal forest. Although Na^+ and Cl^- in the forest floor were high in relation to Na^+ and Cl^- in the mineral soil, they seemed to be low enough that neither tree nor understory plant growth was inhibited. The ability of white spruce (and aspen) to avoid salt accumulation, at least in younger foliage, could potentially be a factor limiting the amount of salts that end up in the forest floor.

4.3.3. Other factors influencing white spruce growth and physiology

4.3.3.1. Edaphic factors

That we found few effects of the different salinity levels on white spruce growth or physiology is surprising because many other studies have found *Picea* spp. to be some of the most salt-sensitive trees; this leads to inquiry about the possible confounding influence of other environmental factors. At Salt Plains, the effect of salinity may have been confounded by highly alkaline conditions in the upper subsoil, or by soil temperature. Even though the EC decreased substantially from the high salinity to low salinity plots (Figure 2.5), the pH of the upper subsoil remained at 9.0 or above (Figure 2.3), so conditions in the low salinity soil may have been no more suitable for trees than conditions in the high salinity soil. The soil temperature decreased substantially at the Salt Plains from the high to low salinity soils (Figure 2.7); lower soil temperatures could have reduced nutrient availability to trees in the low salinity soil, especially nitrogen (Krause 1991), limiting growth in what would otherwise have been more favorable soil conditions.

For all salinity levels at Benchmark, white spruce grew similarly in height, especially in the first 50 years beyond BH age (Figure 4.2). Did environmental variables other than salinity affect tree growth? Moisture availability may have decreased with decreasing salinity at this site because the medium salinity soil was at a mid-slope position and the low salinity soil was at an upper-slope position (Appendix F). Unfortunately, no soil moisture probes were installed at this site, so the only available data were from one day; soil water content was lowest in the low salinity plot, but it was still above the estimated field capacity (Table 2.2). Alkalinity and sodicity could also have confounded the effect of salinity at Benchmark. In the low salinity plots pH levels above 8.5 existed closer to the surface than in the other plots (Figure 2.3), and the lower subsoil sodicity was actually lowest in the high salinity soil (Figure 2.6). Besides salinity, sodicity, alkalinity, and soil water content, there is also the possibility that white spruce at Benchmark were severely limited by N. These trees had foliar N concentrations associated with N deficiency in other studies and less N per needle than trees at the other sites. If N was more limiting than the other unfavorable soil properties, that would explain why tree growth at Benchmark was similar among soils that differed substantially in their chemistry.

Environmental variables other than salinity and sodicity remained relatively consistent from the high to low salinity level at Clearwater. It seems unlikely that the effect of salinity was confounded by other factors, and more likely that high variation in growth among trees obscured any possible influence of salinity. Clearwater was the only site that showed a trend of increasing site index with decreasing salinity, but high variation in height growth within

treatments prevented us from making conclusions about the effects of salinity. Clearwater was not as even-aged as the other study sites, so we were further limited in drawing conclusions on this parameter alone because even-aged stands are an assumption for calculating site index (Monserud 1984). Despite the high variation in growth at Clearwater, white spruce growth was still clearly faster there than at the other sites, suggesting that soil conditions at Clearwater were, in general, more favorable for tree growth than at the other sites. High variation in growth may have been caused by highly heterogeneous soils with many microsites, or by genotypic variation. If genotype was a major factor in growth variation at Clearwater, it would support the idea put forth by Renault et al. (1998, 1999) that genotype is an important factor in salt tolerance, in particular for conifers.

4.3.3.2. Mycorrhizal associations

The critical role of ectomycorrhizae in white spruce growth and nutrition is widely recognized, but we know little about how they may influence salinity tolerance. Mycorrhizal species vary in terms of the benefit conferred to the host tree (Perry et al. 1987) and Kernaghan et al. (2002) documented differences in salt tolerance among mycorrhizal fungi. They recommend three species for use in saline soils: *Laccaria bicolor*, *Hebeloma crustuliniforme*, and *Wilcoxina mikolae*. Subsequently, *H. crustuliniforme* and *L. bicolor* were shown to be benefit white spruce seedlings exposed to salinity (Muhsin and Zwiazek 2002, Nguyen et al. 2006).

We collected no mycorrhizal data in this study, but ectomycorrhizae no doubt influenced growth of white spruce in these saline soils, through improved nutrient and water uptake or by resource sharing through a common mycorrhizal network (Simard and Durall 2004). Findings that white spruce is salt-sensitive may be partly attributable to experiments in which trees were grown without mycorrhizae, or without the most beneficial mycorrhizae. Further examination of the role of mycorrhizal fungi in the salt tolerance of boreal forest trees is warranted and these naturally saline sites could be useful locations for further study of mycorrhizae-plant-salt interactions, or for isolating fungi that tolerate saline conditions.

4.3.3.3. Shallow rooting

White spruce is known to be a relatively shallow-rooted species (Strong and La Roi 1983, Gale and Grigal 1987), which could help it survive on soils that increase in salinity with depth, like the soils of this study. Previous research relating white spruce site index to soil properties found that depth of the rooting zone was the single most important factor in explaining site productivity (Wang 1995). Trees at Benchmark and Salt Plains generally grew slowly; a small amount of rooting space or low quality rooting space would help explain that slow growth. An associated study will directly examine rooting depth and density at these naturally saline sites.

4.4. Conclusions

White spruce has the capability to survive on saline soil, but may not have the capability to be very productive on saline soil. Although white spruce growth seemed unaffected by the different salinity levels and the trees we studied seemed to be less sensitive to salinity than previously reported (Maynard et al. 1996, McKenzie et al. 1993), most stands were considered non-productive. It seems that a multitude of variables, including salinity, limited the productivity of white spruce stands in this study. More or equally important as the total concentration of soluble salts were alkalinity, sodicity, soil temperature, nitrogen availability, and moisture availability.

That we found foliar Na accumulation in only one tree, no Cl accumulation, and no relationship between salinity level and foliar nutrient concentrations or $\delta^{13}C$ suggests that white spruce trees at these study sites were somewhat resistant to ion toxicity, nutrient imbalance, and water deficit; this probably helped them establish on soils with pH > 8.5, EC > 10, and SAR > 13. Foliar $\delta^{15}N$ was the only physiological parameter we measured that was possibly affected by salinity at one site. Foliar $\delta^{15}N$ also showed the strongest effect of treatment in saline aspen stands (Chapter 3), suggesting that there is more potential for interesting relationships between soil salinity and foliar $\delta^{15}N$ than for foliar $\delta^{13}C$ in mature white spruce and aspen.

Table 4.1. Site index of white spruce in high (H), medium (M), and low (L) salinity plots. Benchmark and Clearwater site indexes were the mean of 2 trees per treatment determined with stem analysis. Salt Plains site indexes were the mean of 4 trees per treatment estimated from site index curve equations using the data on total height and breast height age (Huang et al. 1994, Wang and Huang 2000).

	Salinity level		
Site	H	M	L
Benchmark	12.1	12.4	12.8
Clearwater	10.4	14.3	16.3
Salt Plains	5.6	5.7	7.0

Table 4.2. Results of analysis of variance testing for effects of treatment (Trmt equals salinity level), site, and interactions between them on the concentrations of sodium, chloride, macronutrients, and micronutrients, and carbon and nitrogen stable isotope ratios in white spruce needles collected midsummer 2006. P values in bold are significant at the (Bonferroni-adjusted) $\alpha = 0.001$ level.

Variable	Trmt	Site	Trmt×Site
Na	0.68	0.49	0.57
Cl	0.99	0.91	0.67
C	0.92	0.72	0.61
N	0.25	**0.0004**	0.36
P	0.15	0.85	0.53
K	0.84	0.22	0.81
Ca	0.18	0.003	0.31
Mg	0.22	0.24	0.20
S	0.21	0.05	0.90
Mn	0.09	**0.001**	0.52
Fe	0.16	**0.0003**	0.19
Al	0.52	0.005	0.39
Zn	0.47	0.02	0.47
Cu	0.11	0.04	0.03
$\delta^{13}C$	0.45	0.37	0.49
$\delta^{15}N$	0.26	0.14	0.01

Table 4.3. Foliar concentrations (mean ± 95% confidence interval) of the nutrients that were significantly affected by site: nitrogen, manganese, and iron. Samples were from four trees per plot for each high, medium, and low salinity plot within a site. For each nutrient, sites with the same letter are not significantly different at the (Bonferroni-adjusted) $\alpha = 0.001$ level.

	Site		
Variable	Benchmark	Clearwater	Salt Plains
N	0.8^{a}	1.1^{b}	1.0^{b}
	(0.1)	(0.2)	(0.1)
Mn	0.69^{b}	0.26^{a}	0.28^{ab}
	(0.26)	(0.15)	(0.08)
Fe	0.048^{a}	0.047^{a}	0.071^{b}
	(0.007)	(0.005)	(0.015)

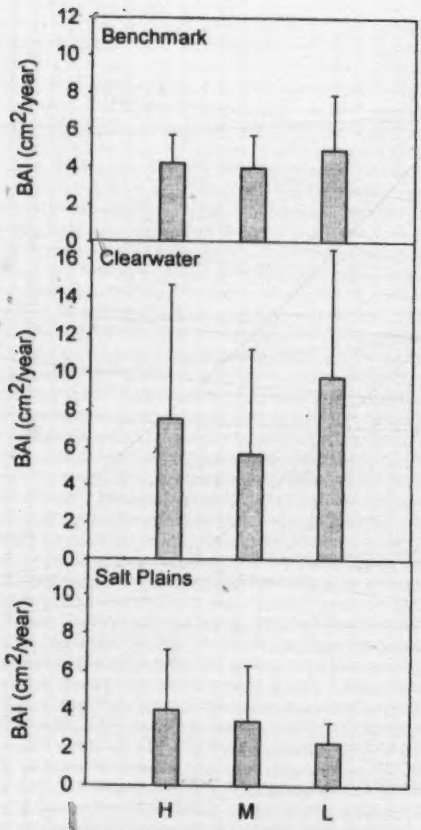

Figure 4.1. White spruce basal area growth rates and 95% confidence intervals for high (H), medium (M), and low (L) salinity plots. Overall basal area growth was significantly higher at Clearwater than at Benchmark or Salt Plains at $\alpha = 0.05$. There were no significant differences among plots for any of the sites.

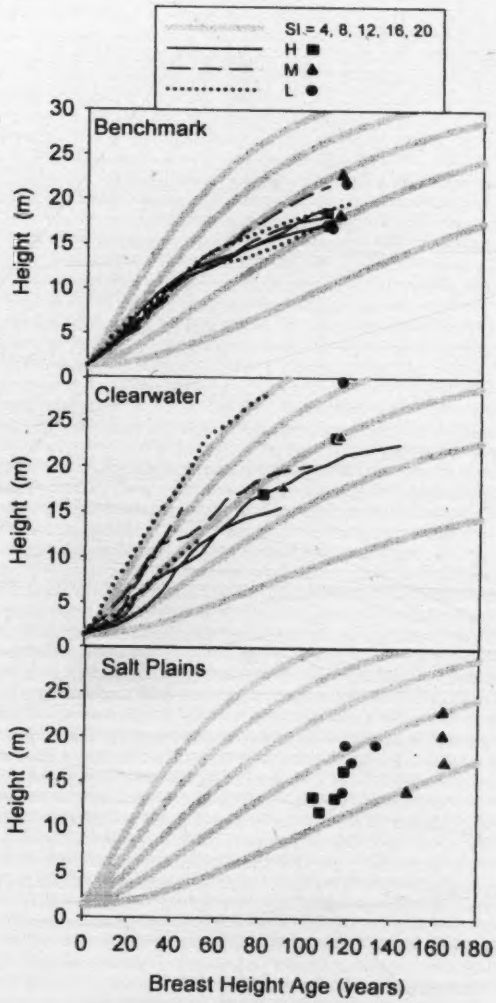

Figure 4.2. White spruce age-height growth curves for 2 trees per high (H), medium (M), and low (L) salinity plot at the Benchmark and Clearwater sites. Additional points are the age and height of cored trees (two trees per plot at Benchmark and Clearwater and four trees per plot at Salt Plains). Gray lines are provincial (Clearwater; Huang et al. 1994) or Northern Mixedwood (Benchmark and Salt Plains; Wang and Huang 2000) growth curves for site indexes of 4, 8, and 12 (non-productive), 16 (low capability), and 20 (high capability; Leskiw 2004).

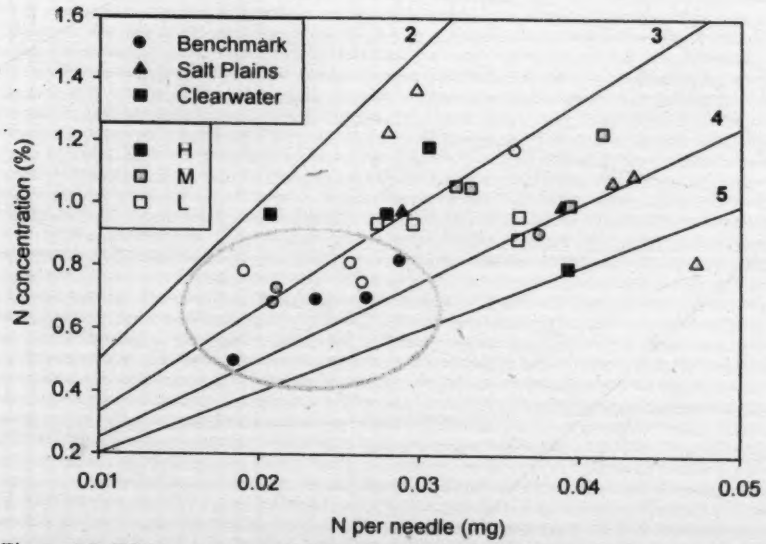

Figure 4.3. White spruce needle nitrogen concentrations as related to nitrogen content in high, medium, and low salinity plots at the three sites. Drawn lines indicate constant weight per needle of 2, 3, 4, and 5 mg. The gray circle indicates the generally lower nitrogen concentrations and contents across leaf weights at Benchmark.

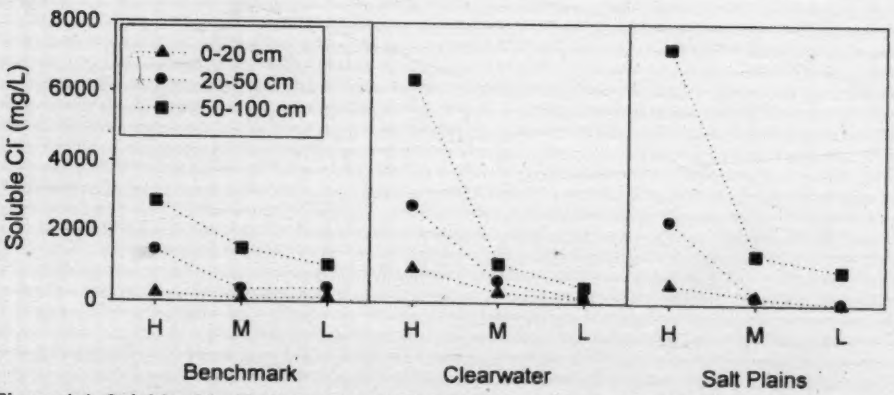

Figure 4.4. Soluble chloride in the topsoil (0-20 cm), upper subsoil (20 – 50 cm), and lower subsoil (50 – 100 cm) in high (H), medium (M), and low (L) salinity plots for white spruce stands at each of the three sites.

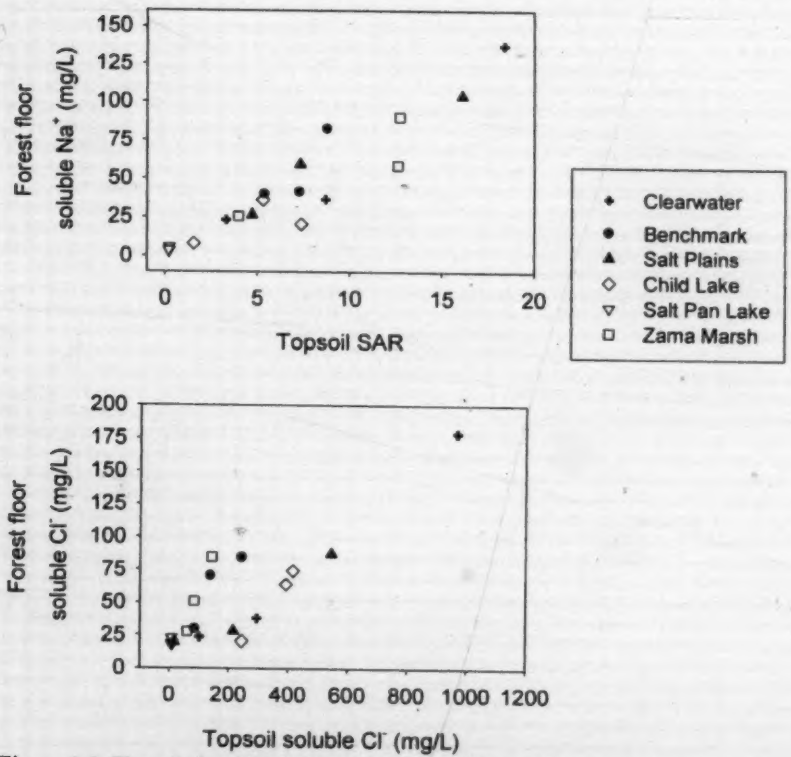

Figure 4.5. The relationships between topsoil and forest floor concentrations of sodium and chloride at white spruce (closed symbols) and aspen (open symbols) naturally saline sites. In both cases there was a significant positive relationship. Sodium: $R^2 = 0.87$ ($p < 0.0001$); chloride: $R^2 = 0.44$ ($p < 0.004$) analyzed without the outlier (~1000 mg/L value).

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Chapter 5. Conclusions

5.1. General summary

This research shows that forests dominated by aspen and white spruce can establish on soils that are moderately to extremely saline at depth, given a natural LFH layer and at least 20 cm of a natural mineral soil profile with EC less than 4 dS/m. Forests growing on saline soils can host diverse plant communities typical of the boreal forest, and occasionally aspen forests can even be productive (i.e., achieving Class 1 land capability [Leskiw 2004]). Likely a rich nutrient regime and mesic to subhygric moisture conditions are necessary for forest establishment on saline sites. Both aspen and white spruce are somewhat tolerant of salinity; neither seemed to experience salinity-related nutrient stress in these saline soils, and both mainly avoided salt ion accumulation in their foliage. Most differences in foliar elemental concentrations in both species could be attributed to the differing soil characteristics among sites, rather than among treatments.

Generally aspen height and basal area growth rate decreased steadily with increasing salinity. White spruce, however, did not show this expected pattern. Only at one white spruce site was there a trend of decreasing site index with increasing salinity. It seemed variables other than salinity (e.g., sodicity, alkalinity, soil water content, soil temperature, nitrogen availability) had a stronger influence on white spruce growth at these sites.

5.2. Differences between aspen and white spruce

Basic differences in growth rates between aspen and white spruce have probably been observed since humans first arrived in North America. A recent laboratory experiment by Khasa et al. (2002) nicely illustrated the difference; after a one month experiment, aspen seedlings from 4 seedlots were >500 mg dry weight while white spruce seedlings were <50 mg. Of equal relevance, every aspen seedling receiving saline irrigation waters died, while 63% of white spruce seedlings in salinity treatments survived. These responses reflect species niches in nature. Aspen is a shade-intolerant species, able to grow quickly above ground and deeply belowground to exploit light, water, and nutrients in early successional environments (Gale and Grigal 1987). White spruce on the other hand, has moderate shade tolerance, and can withstand lower light and nutrient conditions for years in the understory, growing slowly but persistently (Nienstaedt and Zasada 1990). The same story seemed to be true for this study. In a saline environment, aspen could grow 22 m tall in 50 years, but basal area growth was reduced by 50% at higher salinity levels, and aspen was never found growing in soils as saline or sodic as those that white spruce tolerated. White spruce grew slowly, sometimes very slowly, in all salinity levels, and although some trees grew faster than others, overall productivity was low. Generally white spruce growth was not reduced by increasing salinity, in contrast to aspen, and white

spruce were able to survive on soils with higher levels of salinity, sodicity, and alkalinity.

Another difference between these two species, that helps explain the observed differences in survival and growth on saline soils, is their rooting characteristics. Gale and Grigal (1987) reviewed studies on vertical root distributions and found that earlier successional species, such as aspen, generally have deeper root systems than later successional species such as white spruce. Indeed, the average root distributions from their review of the two species differ remarkably (Figure 5.1).

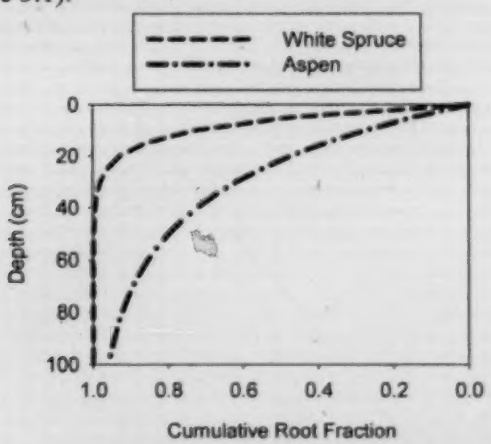

Figure 5.1. Average vertical root distribution of white spruce and aspen roots as reviewed and developed by Gale and Grigal (1987).

Gale and Grigal (1987) suggested that species can change their rooting habit to adapt to different soil conditions, but that such changes represent additional stress on the tree. Since white spruce naturally have shallower root systems than aspen, they are less likely to be stressed in soils that increase in salinity with depth. For aspen to root as shallowly as white spruce, tree stress would increase, and growth would be reduced as a consequence. Generally aspen is thought to deplete soil water more quickly and to a greater depth than conifers like white spruce (Peterson and Peterson 1995) which probably relates to its deeper rooting habit. Strong and La Roi (1983) found that aspen roots were mostly located in the mineral soil, which would allow deeper use of soil water, whereas white spruce roots were primarily in the F and H horizons of the forest floor. These rooting depth patterns can help explain why the two species responded differently to the salinity levels in this study.

5.3. Applications to reclamation

While it is promising that boreal forest communities have been found growing on naturally saline soils, these communities are rare and may also be difficult to establish on engineered soils; generally where high salinity is found,

trees are not. It is likely that a combination of factors allowed the communities in this study to persist on saline soils. A conservative approach to forest reclamation of saline soils is to replicate the soil and groundwater characteristics of existing saline communities as closely as possible.

5.3.1. Soil characteristics

Some recommendations for boreal forest reclamation practices on saline soils can be drawn from this research. Evidently, the electrical conductivity of the topsoil should be below 4 dS/m in constructed soils and constructed landscapes if forest communities are desired. The minimum depth for a layer with this low salinity at naturally saline sites was 20 cm plus the forest floor . It appears as though the salinity of the upper and lower subsoil can be above 4 dS/m, and as high as 23 dS/m (Salt Plains) in the lower subsoil, without precluding the establishment of forest communities under the current climactic conditions. Caution should be used when reclaiming saline soils because we do not fully understand the interactions between climate, soil moisture availability, soil salinity and saline groundwater. The forests examined in this research may be surviving through a delicate balance of evapo-transpiration, precipitation, and water table fluctuations. For example, aspen survive at Zama Marsh regardless of a highly saline water table, but chloride is accumulating in aspen leaves where soil and groundwater chloride are the highest. Higher groundwater chloride, or more frequent rises in the water table, could seriously injure those aspen. During the drought of 2002 in Alberta, aspen and white spruce basal area growth was virtually zero for many of the trees we examined. Consecutive drought years could affect forests on saline soils more strongly than on non-saline forest soils because of increased capillary rise of salts and concentration of remaining salts. Given that drought frequency is likely to increase with global warming such that warmer and drier conditions are expected for the Canadian boreal forest (Hogg 1994) establishment of forests on saline soils may become increasingly difficult. Some of the saline soils examined in this study appeared to be grassland soils and may not have been forested in drier periods (i.e., before 1850), another indication that forest establishment on saline soils may not be possible under some conditions. Thus, this documentation of aspen and white spruce trees surviving on saline soils should not be considered a panacea for salt-affected soil reclamation.

We have learned from these naturally saline sites that forests can establish on saline soils with a medium-rich to rich soil nutrient regime. It is unknown whether forests can tolerate saline soils with fewer nutrients. To use these sites as models for reclamation, constructed soils should contain adequate nutrients and capacity to continually recycle and supply nutrients over time. A conservative approach would be to construct soil with more soil nutrients than what would be required by aspen and white spruce on non-saline soils.

Where forests had established on high salinity soils, the soil moisture regime was subhygric or mesic. Only in medium or low salinity forest stands did we find soil moisture regimes drier than mesic, suggesting that ample soil moisture is necessary for forest growth when salinity is high. The soil water content in most of these stands was close to or above the estimated field capacity,

at least in the upper subsoil, for the whole growing season. Where we did find coarse-textured soil, it was underlain by finer-textured soil, and the total salt concentrations were lower than at the other sites (Salt Pan Lake). If salinity in the subsoil of reclaimed soils is expected to be above 4 dS/m, it seems that fine-textured materials will be necessary to provide adequate moisture for forest development.

Boreal forests can establish where soil characteristics other than salinity are also extreme, such as pH > 8.5 and SAR > 13. Ensuring that the topsoil pH and SAR do not exceed values measured in the topsoil in this study, and that the soil moisture and nutrient regimes are at least as high as those found in this study, will increase the chances of the successful reclamation of sodic and highly alkaline soils, as for saline soils.

5.3.2. Vegetation characteristics

A variety of common boreal forest plants is able to establish on soils that are saline at depth, and a revegetation strategy for constructed soils over saline tailings could be very similar to a strategy for non-saline constructed soil. Normal boreal forest succession seems to be possible on naturally saline soils, so a self-sustaining plant community should be able to establish and develop over time on reclaimed saline soils. The understory plant composition on reforested reclaimed soils will likely be determined by factors other than the salinity of the lower soil depths. Instead the understory plant community will probably reflect processes of species establishment plus the influence of the developing forest canopy, as has been found in non-saline mixedwood forests (Macdonald and Fenniak 2007).

It may be critical to establish vegetation cover and a litter layer immediately on reclaimed sites to prevent evaporative rise of salts. Bare salt-affected flood plains of the Tanana River in interior Alaska quickly developed salt crusts during warm weather, but this was prevented experimentally with a litter layer (Dyrness and Van Cleve 1993). Salt rise was attributed to evaporation from the bare soil surface, and could probably also occur on reclaimed saline soils in Alberta. Similar caution would be appropriate if stands on saline soils are to be harvested. Removal of much of the biomass could change the hydrology enough that salt concentrations could increase in surface soils. This occurred on one white spruce dominated floodplain after clear-cutting and forest floor removal (Yarie 1993). Preventing damage of the forest floor may be an important measure to prevent the evaporative rise of salts after harvest.

5.3.3. Potential aspen growth on reclaimed salt-affected soils

Constructed soils in reclaimed landscapes with soil and nutrient conditions similar to the low salinity soil at Child Lake may be able to support productive aspen growth, even if the lower subsoil is affected by salinity. Where lower portions of the soil are saline, stands should be watched carefully as they age, because growth limitations associated with salinity may not be evident in juvenile stands. As trees age and extend their root systems further into the soil, the trees begin to utilize more of the soil in search of water and nutrients and growth may start to decline, as seemed to occur at these naturally saline sites. Because saline

aspen stands may be quite shallowly rooted, harvesting these stands could put remaining stems at a high risk of windthrow.

An adequate moisture regime seems especially important to aspen growing in high salinity soils, as reduction of aspen growth was observed at lower electrical conductivity in the coarse textured soils of Salt Pan Lake than in the fine textured soils at the other sites. If high electrical conductivity values are expected in the lower subsoil at a reclaimed site, fine textured soil capping material(s) would probably be necessary to support aspen growth. A medium-rich to rich nutrient regime appears to be adequate to support aspen growth in saline soils; there was no evidence of nutritional deficiencies at these sites, although nitrogen uptake may have been affected by salinity. Actual experimental fertilization of saline forest stands would be necessary to make stronger conclusions about possible gains in aspen production by addition of limiting nutrient(s).

We found little evidence for any intra-specific variation in salt tolerance for aspen. Aspen at three very different sites had similarly slow basal area growth in conditions near the upper limit of their salinity tolerance range (high salinity) and it was mainly the medium and low salinity aspen that showed higher variation in basal area growth. Aspen response to salinity, as measured by foliar $\delta^{13}C$ and $\delta^{15}N$, was similar among sites and aspen foliar $\delta^{13}C$ was similar to other aspen in the region – other possible indications that gains in aspen production may not be possible via genetic selection for salt tolerance.

5.3.4. Potential white spruce growth on reclaimed salt-affected soil

At these naturally saline sites, white spruce tolerated higher salinity, sodicity, and alkalinity than expected based on previous laboratory and field trials. The most remarkable examples of salt tolerance were in the high salinity soils at Clearwater and Salt Plains, where even the topsoil was slightly saline and sodic. These examples suggest that white spruce could be used in the revegetation of saline-sodic soils in the oilsand region, as long as the topsoil EC is below 4 dS/m. However, the low productivity of these stands suggests that forestry operations may not be feasible for white spruce stands growing on saline soils. Diverse saline white spruce stands are possible, but productive saline white spruce stands may not be possible.

The high variation in tree growth measured in this study, especially at Clearwater, supports observations in the lab (Renault et al. 1998) that genotypic differences in salt tolerance exist for white spruce. In the reclamation setting where seedlings are nursery raised and then planted, productivity gains on salt affected soil may be made by obtaining and planting the most salt resistant stock. Seed collection from the fastest growing trees in the high salinity soils could be a worthwhile investment. For example, at the Salt Plains, even though average tree growth is slow, some trees were growing more than twice as fast in height and width as others in the same soil. This variation in growth could be due to genotypic differences in salinity tolerance or to genotypic differences in inherent growth rates which would have been observed with or without the influence of salinity. Alternatively, variation in white spruce growth within the same salinity level could have been due to soil heterogeneity. If variation was due to genotypic

differences, a potential doubling in stand productivity could be achieved with the selection of more salt tolerant or fast-growing genotypes.

The possibility that these white spruce stands were limited somewhat by nitrogen, especially at Benchmark, means that proper management of nitrogen on reclaimed sites could potentially increase tree growth. The establishment of ample nutrients and moisture on reclaimed saline soils would reduce the chance for a factor other than salinity to limit tree growth. Anecdotally, it seems possible that white spruce could be productive on saline soils if nutrients and water were plentiful and lower subsoil salinity was in the moderate range (4-8 dS/m). At Saline Lake, the most fertile site in this study, the one white spruce tree at the high salinity level had an estimated height of 14.5 m at 50 years BH age (Huang et al. 1994), which is 2 m taller than other white spruce at the high salinity level. White spruce can potentially grow more quickly on saline soil than we saw in this study, given the right conditions.

5.4. Limitations and Strengths of this Study

The scarcity of previous research on the effects of salinity on mature trees and forest communities makes this study a valuable contribution. During the initial stages of this research we considered the best way to sample these naturally saline sites in order to separate the effect of salinity from other environmental variables. Originally we intended to sample from paired non-saline control landscapes. However, despite much effort, we could not find suitable non-saline stands with soil and vegetation characteristics (other than salinity) similar to the saline stands. Ultimately we decided to sample each site as a separate experiment so that the low salinity level would be the best 'control' possible for the high salinity level. Although there were no true non-saline 'controls' in this study, significant differences among sites in foliar elemental concentrations and corresponding differences in soil chemistry support our decision about the best experimental design to use in this instance. Comparing paired saline 'treatment' sites and similar non-saline 'control' sites would have yielded many differences in tree growth and physiology, but it would be difficult to interpret if they were due to salinity or other factors.

This study was limited by the rarity of naturally saline forested sites, and the small size of forest stands growing on soils of consistent salinity. Our experimental units were individual trees growing within meters of each other and were not truly independent, especially at the aspen sites where trees could have been part of the same clone. However, that we found similar responses to salinity within each set of three sites for each forest type increases the strength of our conclusions. The three sites for each species are truly independent replicates. While this research contributes to our broader understanding of boreal forest development and productivity in saline landscapes, it is also immediately applicable in the practical world of saline soil reclamation.

5.5. Future Directions for Research

The results from this study are promising for the oil and gas industry in that they suggest saline soils can be successfully reclaimed to boreal forest vegetation. The soil and vegetation characteristics of these naturally saline sites can serve as models of what to expect after operational scale reclamation of saline soils. Our results suggest that saline soil reclamation may be possible with less than a meter of clean fill over the saline materials, but that saline stands may be especially vulnerable to changes in climactic and hydrological conditions. Of course, more robust answers to the questions: *i*) What are suitable conditions for long-term plant growth and reproduction? *ii*) What are the minimum suitable conditions for meeting forest productivity targets? and *iii*) Which plant species and genotypes are most suitable for the revegetation of salt-affected soils? need to be addressed in longer-term studies of operational scale reclamation practices.

Additional research examining seed lot differences in salt tolerance could potentially lead to gains in forest productivity on saline soils. Other gainful research might be found in the field of mycorrhizal ecology. Prior and current work in these areas has already been valuable to understanding interactions between plants and salinity in the laboratory, and this could be extended to longer-term field investigations.

Although we found little evidence of interactions between salinity and plant nutritional status, there was some evidence of salinity effects on nitrogen uptake, and nitrogen appeared to be the most limiting nutrient at the white spruce naturally saline sites. Experimental manipulation of nitrogen on saline soils may provide substantiation that tree growth on saline soils is partially limited by nitrogen availability and that nitrogen addition can improve productivity. Further study of the interactions between foliar iron, manganese, and aluminum and soil pH may also advance our understanding of tree nutrition in highly alkaline soils.

More detailed physiological measurements at these naturally saline sites could help us understand what, if any, physiological adjustments mature white spruce and aspen make in saline soils. Measurements of salt ion concentrations in the roots, older foliage, and other tissues of these trees could help us elucidate the mechanisms of salt tolerance expressed by these species.

Rare features of the natural landscape, like these saline sites, are valuable assets for the research community and their protection is continually justified by studies leading to the improved management of our natural resources.

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Appendix A. List of vascular plant species abundance (average % cover) and frequency (% occurrence in plots) in the understory of naturally saline white spruce, aspen, and mixedwood stands. Taxonomy is according to Packer (1983).

	White Spruce		Aspen and Mixedwood	
Species	Abundance	Frequency	Abundance	Frequency
Abies balsamea	7.9	33		
Achillea millefolium	0.2	33	0.4	58
Actaea rubra			0.2	42
Agropyron trachycaulum	6.2	33	1.0	42
Agrostis scabra			0.04	8
Alnus crispa			0.04	8
Alnus tenuifolia	0.1	11		
Amelanchier alnifolia	0.3	33	5.2	100
Aralia nudicaulis	1.0	33	1.3	25
Arctostaphylos uva-ursi			0.6	17
Aster ciliolatus	0.1	11	1.1	75
Aster conspicuus			0.1	17
Aster laevis	0.1	11	0.1	25
Aster puniceus	0.1	11		
Betula pumila	0.1	11		
Betula glandulosa	2.0	11		
Betula papyrifera	0.8	33		
Calamagrostis canadensis	0.4	22	1.4	58
Campanula rotundifolia			0.04	8
Carex sp.			0.2	17
Carex atheroides	0.1	11		
Circea alpina	0.1	11	0.04	8
Cicuta maculata	0.1	11		
Cornus canadensis	0.7	67	3.3	67
Cornus stolonifera	0.1	22	4.2	25
Delphinium glaucum			0.04	8
Eleagnus commutata	0.1	11	0.04	8
Elymus innovatus	2.0	67	3.1	50
Epilobium angustifolium	0.8	56	6.3	50
Equisetum arvense	0.1	22	0.2	42
Equisetum pratense			0.1	25
Equisetum scirpoides			0.04	8
Festuca ovina			0.04	8
Fragaria vesca			0.5	25
Fragaria virginiana	0.1	11	2.6	83
Galium boreale	0.4	56	1.4	100
Galium triflorum	0.1	11	0.1	25

Appendix A continued...

Geocaulon lividum	1.1	78	0.8	33
Geum triflorum			0.04	8
Hedysarum alpinum	0.3	56	0.04	8
Hieracium umbellatum			0.3	50
Juncus balticus	0.2	11	0.6	8
Juniperus communis	0.2	11		
Juniperus horizontalis	4.2	22		
Lathyrus ochroleucus	0.2	33	1.2	92
Ledum groenlandicum	11.2	33		
Linnaea borealis	4.1	100	1.0	50
Lonicera involucrata	0.1	11	0.7	83
Maianthemum canadense	0.1	22	0.7	67
Mertensia paniculata			0.4	25
Mitella nuda	0.3	22	0.3	25
Orthilia secunda	0.4	56	0.2	42
Oryzopsis asperifolia			0.1	17
Parnassia palustris	0.1	11		
Petasites frigidus			0.04	8
Petasites palmatus	0.6	44	0.2	33
Picea glauca	0.3	33	0.5	67
Populus balsamifera	0.1	11	0.1	17
Populus tremuloides	2.2	67	3.8	92
Potentilla fruticosa			0.04	8
Prunus virginiana			0.2	17
Pyrola asarifolia	0.1	11	0.7	58
Ribes glandulosum	0.1	11		
Ribes lacustre	0.1	11		
Ribes oxycanthoides	0.2	33	0.5	42
Ribes triste			0.5	25
Rosa acicularis	5.3	100	13.0	100
Rubus arcticus	0.1	11		
Rubus ideaus	0.1	11	0.2	17
Rubus pubescens	1.0	56	1.5	75
Salix sp.	0.7	67	2.6	67
Schizachne purpurascens			0.2	8
Sheperdia canadensis	3.0	44	2.7	67
Smilacina stellata	0.1	22	0.04	8
Solidaga canadensis	0.1	11	0.6	17
Solidaga missouriensis			0.04	8
Sonchus sp.	0.1	22	0.1	25
Symphoricarpos albus	0.3	22	0.8	67

Appendix A continued...

Symphoricarpos occidentalis			1.3	25
Taraxacum officinale			0.04	8
Thalictrum venulosum	0.1	11	0.3	42
Trientalis borealis	0.1	22	0.1	17
Triglochlin palustris	0.1	11		
Urtica dioica	0.1	11		
Vaccinium vitis-idaea	4.1	67	1.1	25
Viburnum edule	0.4	44	7.0	58
Vicia americana			0.7	83
Viola renifolia	0.1	11	0.1	25
Unknown			0.04	8

Appendix B. Bulk density, horizon thickness, gravimetric moisture after air drying, and soil texture of soil horizons in high (H), medium (M), and low (L) salinity plots at the study sites. Soils were classified according to the Canadian System of Soil Classification (Soil Classification Working Group 1998) and Fox et al. (1987).

Site	Salinity Level	Horizon Name	Horizon Depth	Bulk Density (g/cm3)	Horizon Thickness (cm)	Air Dry Gravi. Moist.	Soil Texture*
Benchmark	H	LFH		0.1	6	0.134	
		Aej	0-5	0.9	5	0.035	SiL
		Bntgj1	5-20	1.5	15	0.026	L
		Bntgj2	20-30	nd	20	0.029	L
		Ckgj	30-50	1.5	20	0.028	L
		Ccasg	50-100	1.4	50	0.022	SiL
	M	LFH		0.04	15	0.135	
		Bnt	0-20	1.3	20	0.034	L
		BC	20-35	1.3	15	0.039	SL
		Ck	35-50	1.5	15	0.033	L
		Ccas	50-100	1.5	50	0.029	SiL
	L	LFH		0.1	9	0.131	
		Ae	0-10	1.2	10	0.018	SiL
		AB	10-17	1.2	7	0.020	SiL
		Bnt	17-30	1.5	13	0.022	L
		Ck	30-50	1.4	20	0.028	L
		Cca	50-100	1.4	50	0.020	SiL
Clearwater	H	LF		0.1	16	0.149	
		Fq	0-10	0.1	20	0.162	
		Fw	10-20	0.1	10	0.173	
		Hws	20-30	0.2	10	0.167	
		Csg1	30-50	1.3	20	0.048	L
		Csg2	50-100	nd	50	0.043	L
	M	LF		0.1	17	0.127	
		Fq	0-10	0.1	10	0.160	
		Hw	10-25	0.1	15	0.185	
		C	25-45	1.2	20	0.043	L
		Cg	45-100	nd	55	0.040	L
	L	LF		0.1	15	0.136	
		Fq	0-15	0.1	15	0.180	
		C1	15-25	0.8	10	0.038	L
		Hw	25-40	0.2	15	0.172	
		C2	40-50	0.8	10	0.040	L
		Cg	50-100	nd	50	0.039	L
Salt Plains	H	LF		0.03	7	0.115	
		Ahk	0-17	0.5	17	0.070	SiL
		Ck1	17-45	1.5	28	0.024	SiL
		Ck2	45-70	1.7	25	0.022	SiL
		Ckg	70-100	1.5	30	0.028	SiC
	M	LFH		0.1	12	0.159	
		Ahk	0-13	0.6	13	0.104	SiL

Appendix B continued...

		Ck1	13-50	1.5	37	0.019	SiL
		Ck2	50-90	1.5	40	0.013	SiL
		Ckg	90-100	nd	10	0.018	SiL
	L	LFH		0.1	15	0.149	
		Ahk	0-20	0.5	20	0.076	SiL
		Ck1	20-50	1.1	30	0.023	SiL
		Ck2	50-100	1.5	50	0.017	SiL
Child Lake	H	LFH		0.1	5	0.114	
		Ahe	0-10	1.0	10	0.050	SiL
		Ae	10-22	1.3	22	0.018	L
		Bnt	22-35	1.3	23	0.035	SL
		Ccas	35-50	1.6	15	0.029	SiL
		Bnt^{T}	45-55	1.7			
		Cks	50-100	1.3	50	0.039	SiC
	M	LFH		0.1	6	0.131	
		Aeg	0-15	1.5	15	0.015	L
		Bnt	15-27	1.5	12	0.038	SiL
		Ccagj	27-50	1.4	23	0.024	SiCL
		Ccasg	50-100	1.4	50	0.028	SiCL
	L	LFH		0.1	6	0.151	
		Aegj	0-12	1.1	12	0.019	SiL
		Btgj	12-30	1.3	18	0.035	SiCL
		Ccagj	30-50	1.3	20	0.026	SiCL
		Ccag	50-100	1.4	50	0.026	SiL
Salt Pan Lake	H	LF		0.1	10	0.137	
		Ahj	0-5	0.7	5	0.021	SL
		Ae	5-10	0.7	10	0.006	LS
		Bm	10-25	1.5	15	0.007	S
		IICca1	25-50	1.4	25	0.033	CL
		IICca2	50-100	1.3	50	0.031	SiCL
		IICca3	100-130	nd	30		
	M	LFH		0.1	10	0.123	
		Ahj	0-5	0.9	5	0.022	SL
		Aej	5-9	0.9	4	0.008	LS
		Bm	9-25	1.3	16	0.003	S
		Cca	25-60	1.5	35	0.000	S
		IICca	60-100	1.5	40	0.023	CL
	L	LFH		0.1	10	0.136	
		Ahe	0-8	0.7	8	0.022	SL
		Bm	8-25	1.4	17	0.005	S
		Ck	25-60	1.5	35	0.003	S
		IICca	60-100	1.5	40	0.031	L
Zama Marsh	H	LFH		0.3	5	0.168	
		Ahe	0-5	1.2	5	0.077	C
		Bntgj	5-20	1.3	15	0.075	C
		BCkgj	20-40	1.4	20	0.065	L
		Ccasgj	40-60	nd	20	0.076	SiCL

Appendix B continued...

		Ccasg	60-100	1.4	40	0.070	SiC
	M	LFH		0.1	7	0.140	
		Bntgj	0-20	1.2	20	0.059	C
		Bck	20-35	1.3	15	0.059	L
		Ccasg1	35-50	1.4	15	0.056	SiCL
		Ccasg2	50-100	1.4	50	0.048	SiC
	L	LF		0.1	7	0.143	
		Aegj	0-5	1.2	5	0.033	CL
		Bntg	5-20	1.5	15	0.044	C
		BCg	20-50	1.4	30	0.074	Heavy C
		Ccasg	50-100	1.4	50	0.048	SiC
Saline Lake	H	LFH		0.1	5	0.111	
		Ch	0-20	0.7	20	0.065	SiL
		Ch	20-40	0.7	40	0.060	L
		Chgj	40-80	0.9	40	0.050	SiL
		Csg	80-100	nd	20	0.035	L
	M	LFH		0.2	7	0.105	
		Ch1	0-20	0.6	20	0.058	CL
		Ch2	20-50	0.9	30	0.056	SiL
		Chs	50-70	1.3	20	0.058	SiL
	L	LFH		0.2	5	0.116	
		Ch1	0-20	0.6	20	0.050	L
		Ch2	20-45	0.9	25	0.050	SiL

*SiL-Silt Loam; L-Loam; SiC-Silty Clay; SiCL-Silty Clay Loam; SL-Sandy Loam; LS-Loamy Sand; S-Sand; C-Clay; CL-Clay Loam; L-Loam

†This horizon was missed in the first soil description because the soil was so wet

nd = parameter not determined analytically

Appendix B References

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agriculture and Agri-Food Canada, Ottawa, Ontario.

Fox, C.A., Trowbridge, R., and Tarnocai, C. 1987. Classification, macromorphology and chemical characteristics of folisols from British Columbia. Canadian Journal of Soil Science 67: 765-778.

Appendix C. Soil reaction (pH), electrical conductivity (EC), saturation percent (SP), sodium absorption ratio (SAR), and soluble cations for soil profiles of high (H), medium (M), and low (L) salinity plots at the study sites. Soils were classified according to the Canadian System of Soil Classification (Soil Classification Working Group 1998) and Fox et al. (1987).

Site	Salinity Level	Horizon Name	Horizon Depth	pH	EC (dS/m)	SP (%)	SAR	Soluble cations (mg/L)			
								K^+	Na^+	Mg^{2+}	Ca^{2+}
Benchmark	H	LFH		4.2	0.7	484	3.2	35	82	7	39
		Aej	0-5	4.8	0.9	67	6.3	2	149	5	35
		Bntgj1	5-20	5.8	1.1	44	10	1	231	3	38
		Bntgj2	20-30	7.1	1.5	57	15	1	305	2	27
		Ckgj	30-50	7.8	3.0	72	27	1	580	3	31
		Ccasg	50-100	8.7	10	85	25	4	766	9	55
	M	LFH		4.8	0.5	690	1.2	49	41	8	74
		Bnt	0-20	5.1	0.5	55	7.3	1	101	2	12
		BC	20-35	6.4	1.0	78	10	1	197	2	24
		Ck	35-50	7.9	1.9	81	21	1	395	4	21
		Ccas	50-100	8.7	5.2	97	42	2	967	6	31
	L	LFH		5.4	0.8	572	1.0	83	40	15	94
		Ae	0-10	4.7	0.6	45	3.5	5	82	9	26
		AB	10-17	5.3	0.7	36	6.5	2	113	4	17
		Bnt	17-30	6.2	0.8	54	8.9	1	171	3	23
		Ck	30-50	8.7	2.1	64	17	1	434	9	33
		Cca	50-100	8.7	3.7	84	35	3	720	7	21
Clearwater	H	LF		5.6	1.1	555	4.0	41	137	21	54
		Fq	0-10	5.9	3.3	499	15	20	579	27	67
		Fw	10-20	6.6	4.9	469	22	12	904	34	76
		Hws	20-30	7.1	7.2	336	28	10	1390	47	114
		Csg1	30-50	7.5	10	84	44	14	2066	48	86
		Csg2	50-100	7.4	19	82	70	35	4313	70	170

Appendix C continued...

	M	LF		3.9	0.8	524	0.8	63	36	22	116
		Fq	0-10	4.6	1.0	487	5.2	12	179	17	62
		Hw	10-25	7.5	2.4	415	12	6	436	22	62
		C	25-45	7.9	2.5	69	15	5	453	16	44
		Cg	45-100	7.6	4.2	64	23	8	800	24	54
	L	LF		5.3	0.5	567	0.8	45	23	17	40
		Fq	0-15	5.6	1.0	454	3.5	9	138	31	67
		C1	15-25	7.3	0.6	65	2.5	6	92	26	61
		Hw	25-40	7.0	1.1	324	4.0	5	153	28	65
		C2	40-50	7.4	1.2	59	7.2	4	206	16	37
		Cg	50-100	7.4	2.2	60	16	6	386	12	25
Salt Plains	H	LF		5.7	0.9	423	2.7	31	104	17	85
		Ahk	0-17	8.1	1.9	118	12	1	393	9	68
		Ck1	17-45	9.0	6.9	52	37	4	1428	17	88
		Ck2	45-70	8.7	13	57	57	2	2907	30	146
		Ckg	70-100	8.4	29	56	67	6	5427	72	374
	M	LFH		5.2	0.6	459	1.8	31	59	11	63
		Ahk	0-13	6.9	0.8	97	5.8	0	160	8	45
		Ck1	13-50	9.4	1.5	40	10	6	348	8	85
		Ck2	50-90	9.4	3.9	39	26	8	745	6	51
		Ckg	90-100	8.9	9.8	50	71	3	2217	10	57
	L	LFH		5.6	0.6	637	0.8	67	26	9	70
		Ahk	0-20	7.4	0.9	104	4.7	1	167	13	75
		Ck1	20-50	9.2	0.9	46	5.8	1	220	9	94
		Ck2	50-100	9.3	3.2	40	23	5	680	9	53

Appendix C continued...

Child Lake	H	LFH		5.7	0.9	356	0.4	33	21	37	115
		Ahe	0-10	5.3	1.5	107	3.0	2	148	39	119
		Ae	10-22	6.2	2.3	37	12	1	399	21	52
		Bnt	22-35	8.5	3.5	53	18	1	683	29	60
		Ccas	35-50	8.8	5.6	68	22	1	1089	62	88
		Cks	50-100	8.2	15	68	22	5	2793	397	589
	M	LFH		5.5	0.7	467	1.1	38	36	19	58
		Aeg	0-15	6.2	1.6	33	4.2	9	176	33	80
		Bnt	15-27	8.3	1.9	65	8.7	5	313	27	56
		Ccagj	27-50	8.3	5.4	60	13	8	842	92	152
		Ccasg	50-100	8.1	9.7	66	16	11	1593	234	334
	L	LFH		5.7	0.6	488	0.2	48	8	23	73
		Aegj	0-12	5.6	0.7	38	1.1	19	38	19	58
		Btgj	12-30	7.5	1.6	59	2.2	11	119	53	134
		Ccagj	30-50	7.9	4.3	60	6.2	11	461	125	215
		Ccag	50-100	7.8	7.8	62	9.1	11	951	285	356
Salt Pan Lake	H	LF		5.5	0.8	545	0.1	91	3	24	85
		Ahj	0-5	5.0	0.2	57	0.1	3	3	8	29
		Ae	5-10	5.5	0.1	33	0.2	2	4	5	17
		Bm	10-25	6.4	0.2	33	0.3	2	6	9	23
		IICca1	25-50	8.3	1.8	77	6.0	1	238	30	68
		IICca2	50-100	8.4	3.5	83	12	1	539	41	75
		IICca3	100-130		4.6	96	18	3	758	33	76
	M	LFH		5.7	0.8	464	0.1	72	6	24	118
		Ahj	0-5	5.8	0.3	73	0.2	3	8	17	70
		Aej	5-9	7.2	0.5	39	0.2	1	7	21	101
		Bm	9-25	8.0	0.3	36	0.2	1	8	10	63
		Cca	25-60	8.3	0.3	34	0.4	0	11	9	41
		IICca	60-100	8.3	2.6	82	11	3	411	25	68

Appendix C continued...

	L	LFH		5.9	0.8	549	0.1	78	4	26	86
		Ahe	0-8	6.2	0.4	58	0.2	2	6	16	58
		Bm	8-25	7.8	0.3	36	0.2	0	5	10	46
		Ck	25-60	8.3	0.2	34	0.3	0	7	8	32
		IICca	60-100	8.5	2.1	62	14	3	337	10	30
Zama Marsh	H	LFH		5.6	0.8	360	1.5	36	59	32	56
		Ahe	0-5	5.7	1.2	85	9.1	2	224	12	26
		Bntgj	5-20	6.5	1.6	81	14	1	311	13	18
		BCkgj	20-40	8.3	4.8	98	20	1	1012	70	71
		Ccasgj	40-60	8.2	8.9	109	18	3	1871	283	387
		Ccasg	60-100	8.2	8.8	112	16	6	1728	269	393
	M	LFH		4.6	1.3	532	1.8	79	90	66	90
		Bntgj	0-20	5.2	3.0	78	13	2	521	54	38
		Bck	20-35	7.5	5.8	100	18	1	1169	141	85
		Ccasg1	35-50	8.4	6.3	102	17	2	1207	161	110
		Ccasg2	50-100	8.1	8.2	116	13	8	1394	317	390
	L	LF		5.0	0.1	565	0.6	96	25	38	64
		Aegj	0-5	5.0	0.4	48	2.7	7	48	8	11
		Bntg	5-20	5.3	0.4	49	4.4	2	63	5	8
		BCg	20-50	5.7	1.8	107	8.7	2	289	35	26
		Ccasg	50-100	8.1	5.4	100	10	6	811	229	171
Saline Lake	H	LFH		6.7	1.0	341	0.1	19	2	14	52
		Ch	0-20	7.2	1.1	141	2.1	6	98	26	123
		Ch	20-40	7.7	4.5	115	6.1	3	486	83	348
		Chgj	40-80	8.2	3.8	80	11	2	593	38	156
		Csg	80-100	8.1	5.2	57	14	2	843	51	191

Appendix C continued...

M	LFH		7.2	1.1	266	0.2	56	8	31	164
	Ch1	0-20	7.3	0.7	108	0.2	16	9	23	124
	Ch2	20-50	7.8	1.0	nd	2.1	4	96	23	115
	Chs	50-70	7.7	4.9	90	4.0	3	382	119	493
L	LFH		6.6	0.9	348	0.0	65	2	30	136
	Ch1	0-20	7.4	0.7	106	0.2	14	10	30	134
	Ch2	20-45	7.8	0.6	81	0.6	5	28	20	112

nd = parameter not determined analytically

Appendix C References

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agriculture and Agri-Food Canada, Ottawa, Ontario.

Fox, C.A., Trowbridge, R., and Tarnocai, C. 1987. Classification, macromorphology and chemical characteristics of folisols from British Columbia. Canadian Journal of Soil Science **67:** 765-778.

Appendix D. Total carbon and nitrogen, carbon to nitrogen ratio, mineralizable nitrogen (Min-N), and total cation exchange capacity (CEC) for the top 20 cm of the mineral soil plus the LFH layer of soils in high (H), medium (M), and low (L) salinity plots at the study sites. Mineralizable nitrogen is the total ammonium released after storage and a 2 week anaerobic incubation at 30° C. Cation exchange capacity is the amount of ammonium adsorbed to soil particles and then displaced with sodium chloride. Soils were classified according to the Canadian System of Soil Classification (Soil Classification Working Group 1998) and Fox et al. (1987).

Site	Salinity Level	Horizon Name	Horizon Depth	Total C (%)	Total N (%)	C:N	Min-N (mg/g)	Total CEC (meq/100g)
Benchmark	H	LFH		46	1.5	31	0.37	
		Aej	0-5	5.9	0.27	22	0.02	20
		Bntgj1	5-20	1.9	0.13	15	0.01	1.7
	M	LFH		54	1.5	37	0.57	
		Bnt	0-20	1.8	0.12	15	0.01	21
	L	LFH		48	1.9	25	0.87	
		Ae	0-10	3.2	0.13	26	0.01	11
		AB	10-17	1.2	0.08	16	0.01	12
		Bnt	17-30	1.1	0.09	12	0.005	16
Clearwater	H	LF		53	2.1	26	0.73	
		Fq	0-10	52	2.2	24	0.29	
		Fw	10-20	51	2.5	21	0.25	
	M	LF		53	2.0	27	0.21	
		Fq	0-10	53	2.4	22	0.17	
		Hw	10-25	46	2.3	19	0.26	
	L	LF		51	2.1	25	0.41	
		Fq	0-15	49	2.5	20	0.26	
		C1	15-25	4.1	0.39	11	0.05	26
Salt Plains	H	LF		46	1.8	26	0.69	
		Ahk	0-17	7.4	0.69	11	0.07	43
		Ck1	17-45	0.9	0.12	7	0.001	12

Appendix D continued...

	M	LFH		48	1.9	25	0.60	
		Ahk	0-13	9.2	0.78	12	0.05	51
		Ck1	13-50	1.2	0.09	13	0	11
	L	LFH		57	2.5	23	1.1	
		Ahk	0-20	9.3	0.68	14	0.06	53
Child Lake	H	LFH		38	2.6	15	1.0	
		Ahe	0-10	9.1	0.84	11	0.13	33
		Ae	10-22	1.1	0.11	10	0.001	12
	M	LFH		46	2.2	21	0.95	
		Aeg	0-15	0.8	0.10	8	0.01	8.0
		Bnt	15-27	0.9	0.16	6	0.01	19
	L	LFH		55	2.7	20	0.88	
		Aegj	0-12	1.2	0.14	8	0.02	11
		Btgj	12-30	0.8	0.14	6	0.01	19
Salt Pan Lake	H	LF		60	3.2	19	1.3	
		Ahj	0-5	4.1	0.30	13	0.06	17
		Ae	5-10	0.6	0.08	8	0.01	3.8
		Bm	10-25	0.5	0.07	6	0.01	4.0
	M	LFH		48	2.8	17	1.1	
		Ahj	0-5	4.2	0.36	12	0.06	21
		Aej	5-9	1.2	0.13	9	0.02	7.6
		Bm	9-25	0.5	0.08	6	0.003	4.3

Appendix D continued...

	L	LFH		47	3.0	16	1.2	
		Ahe	0-8	3.3	0.31	11	0.03	19
		Bm	8-25	0.5	0.07	6	0.002	3.9
Zama Marsh	H	LFH		39	2.4	16	1.4	
		Ahe	0-5	6.6	0.54	12	0.14	33
		Bntgj	5-20	3.6	0.33	11	0.05	33
	M	LFH		49	2.4	21	0.56	
		Bntgj	0-20	3.2	0.28	12	0.01	31
	L	LF		54	2.4	22	1.2	
		Aegj	0-5	3.3	0.24	14	0.06	18
		Bntg	5-20	1.7	0.16	10	0.01	20
Saline Lake	H	LFH		38	2.2	17	0.89	
		Ch	0-20	11	0.75	15	0.26	48
	M	LFH		32	1.9	17	0.61	
		Ch1	0-20	7.3	0.46	16	0.21	43
	L	LFH		40	2.3	17	0.95	
		Ch1	0-20	7.5	0.45	17	0.21	45

Appendix D References

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agriculture and Agri-Food Canada, Ottawa, Ontario.

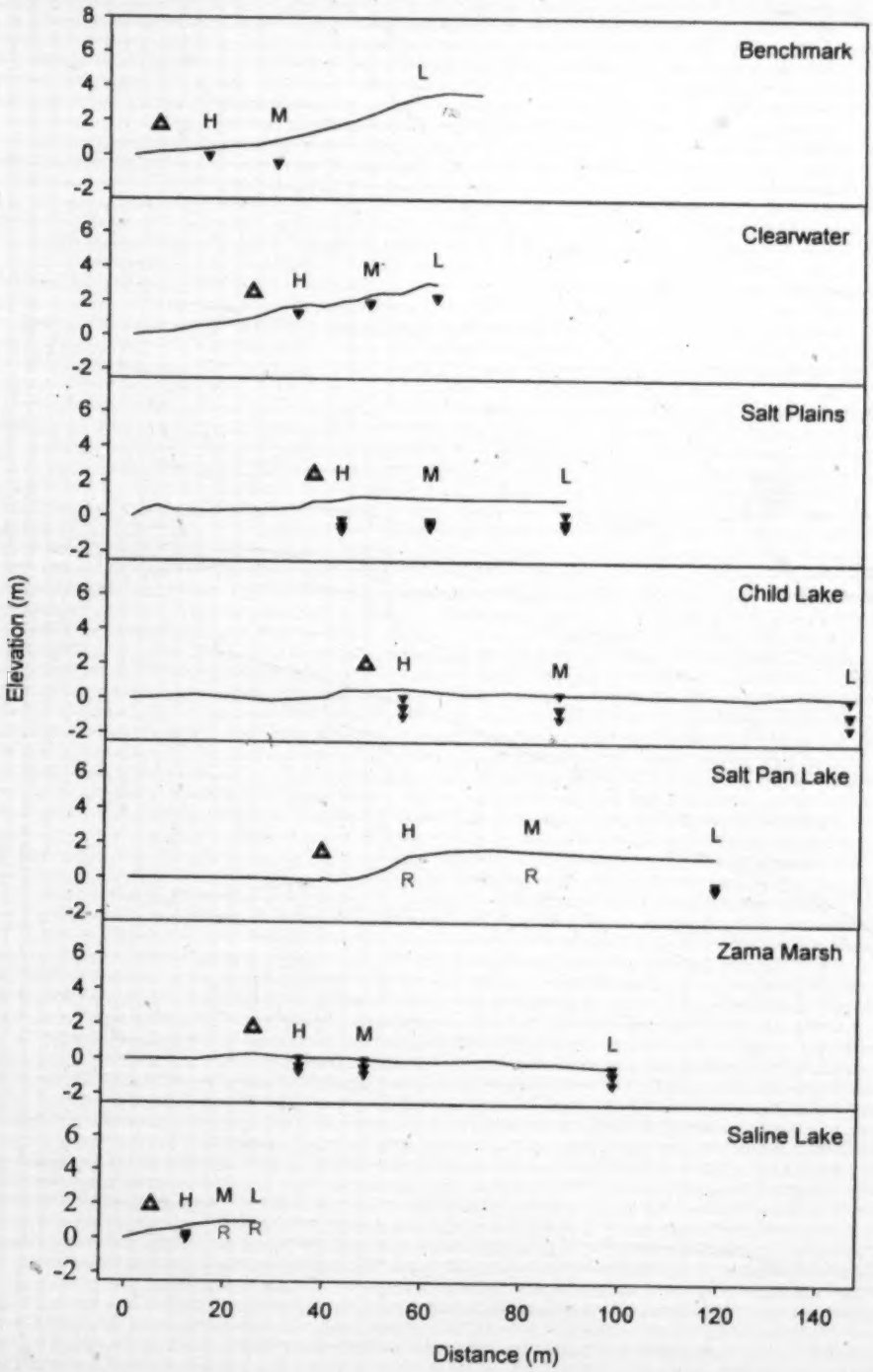
Fox, C.A., Trowbridge, R., and Tarnocai, C. 1987. Classification, macromorphology and chemical characteristics of folisols from British Columbia. Canadian Journal of Soil Science **67:** 765-778.

Appendix E. Determinations of pH, electrical conductivity (EC), and main soluble ions in groundwater samples collected for high (H), medium (M), and low (L) salinity plots at which depth to groundwater was less than 2 m.

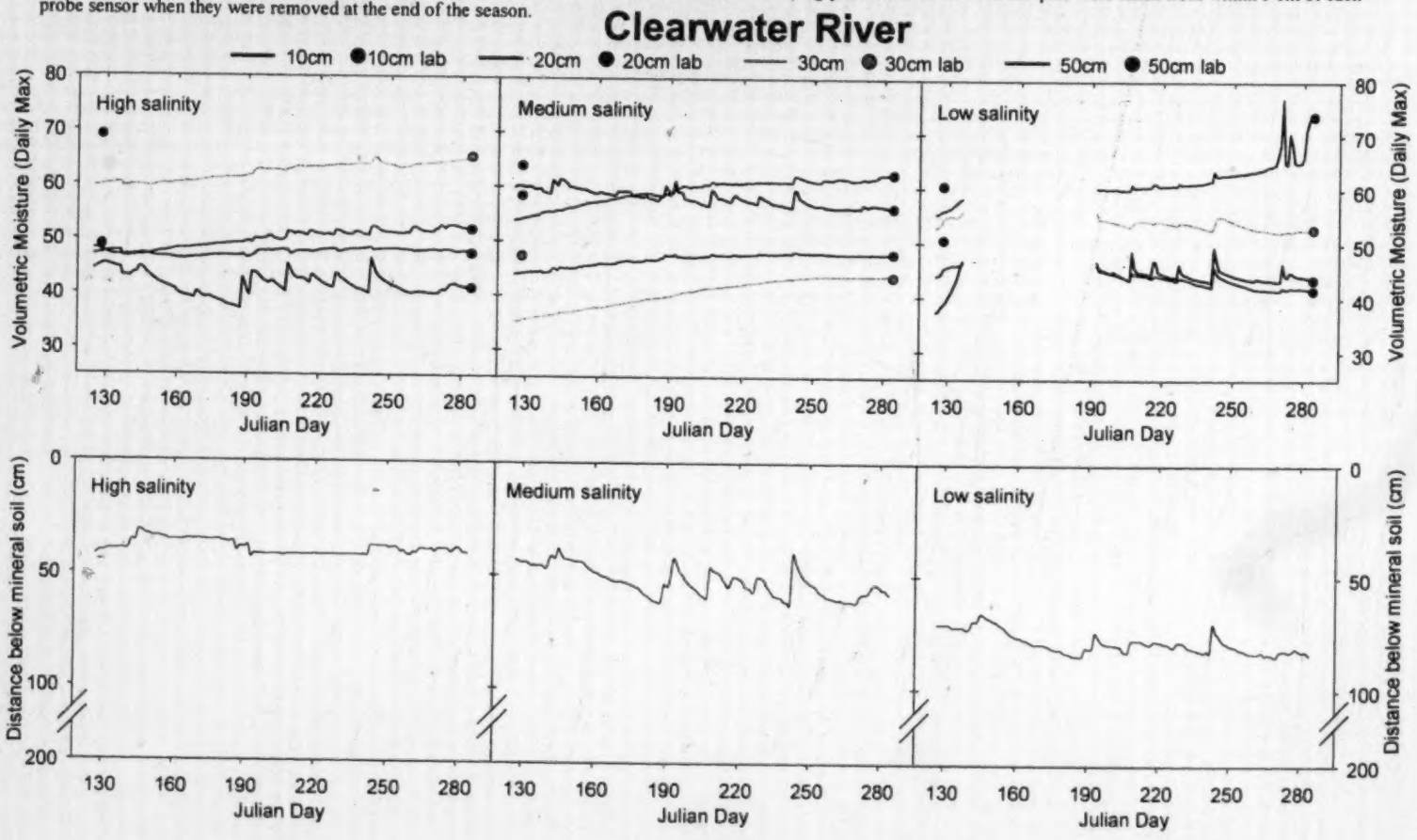
Site	Salinity Level	Groundwater Depth (cm)	pH	EC (dS/m)	Cations (mg/L)					Anions (mg/L)		
					Na^+	K^+	Mg^{2+}	Ca^{2+}	NH_4^+	Cl^-	SO_4^{2-}	HCO_3^-
Benchmark	H	41	7.1	36	4920	5.1	62	188	31	7700	753	251
	M	142	7.1	42	5630	7.5	63	197	58	9300	659	189
Clearwater	H	38	7.1	25	4410	18.9	128	239	6.7	7000	883	339
	M	43	7.2	6.4	430	0.1	22	34	0.5	570	174	128
	L	78	6.7	10	1190	7.9	44	49	2.7	1600	307	268
Salt Plains	H	140	6.9	77	23000	21.7	591	2260	243	43000	1600	230
	M	138	7.4	52	9100	8.4	173	748	55	16000	572	203
Child Lake	H	150	7.5	37	4450	8.0	708	235	BDL	7200	3710	257
	M	115	7.5	11	945	5.6	173	282	8.5	1400	1070	163
	L	146	7.0	6.5	352	0.1	105	135	2.0	770	248	128
Salt Pan Lake	L	188	7.1	8.5	1940	6.7	94	197	BDL	3000	833	296
Zama Marsh	H	56	7.4	16	2140	0.1	259	170	BDL	660	4490	596
	M	50	7.6	13	922	0.1	170	111	BDL	330	2120	227
	L	74	7.4	9.3	1900	5.0	334	200	BDL	1400	3650	643
Saline Lake	H	87	6.9	5.0	900	0.1	80	177	BDL	1500	120	418

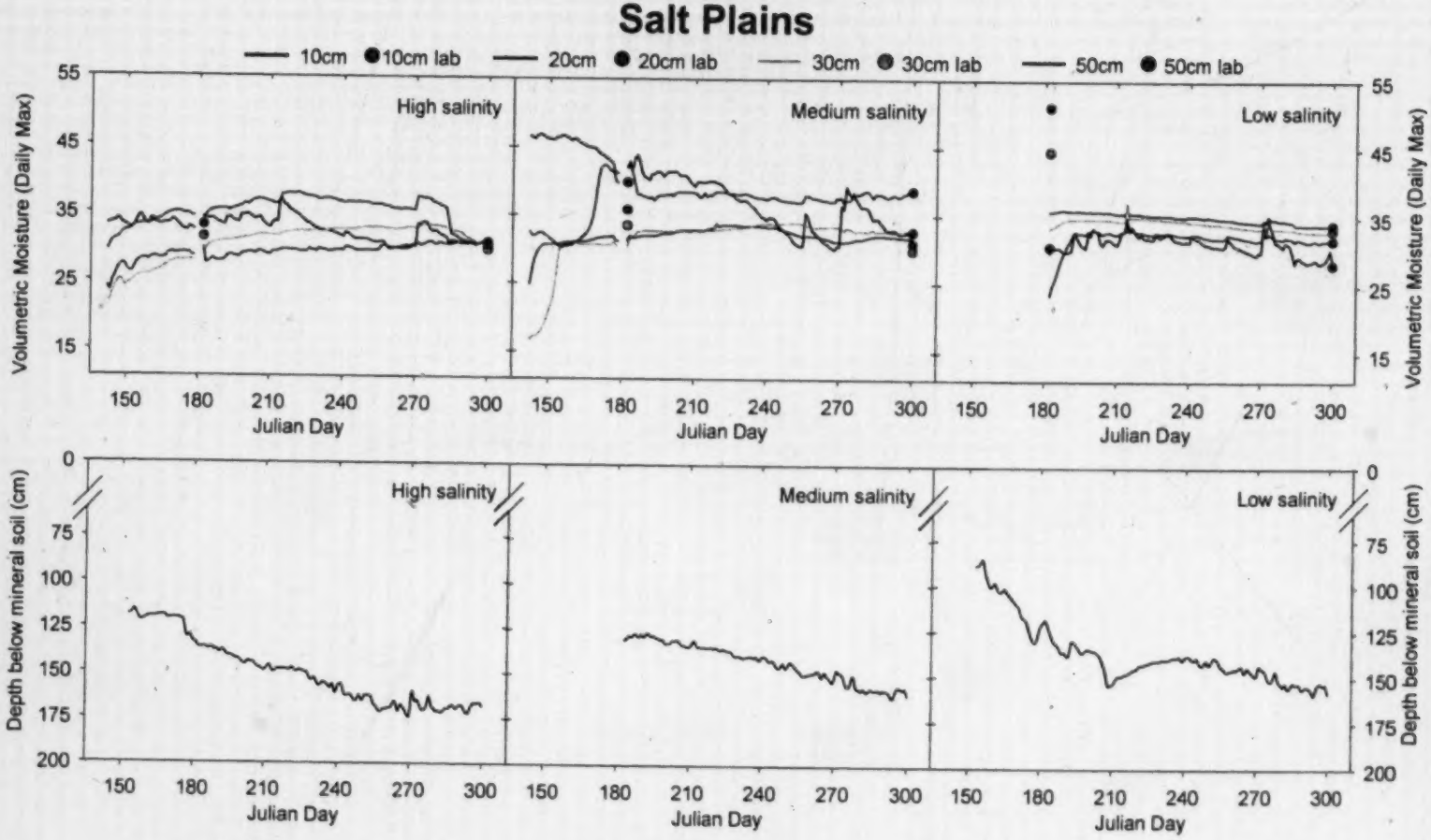
BDL = Below detection limit

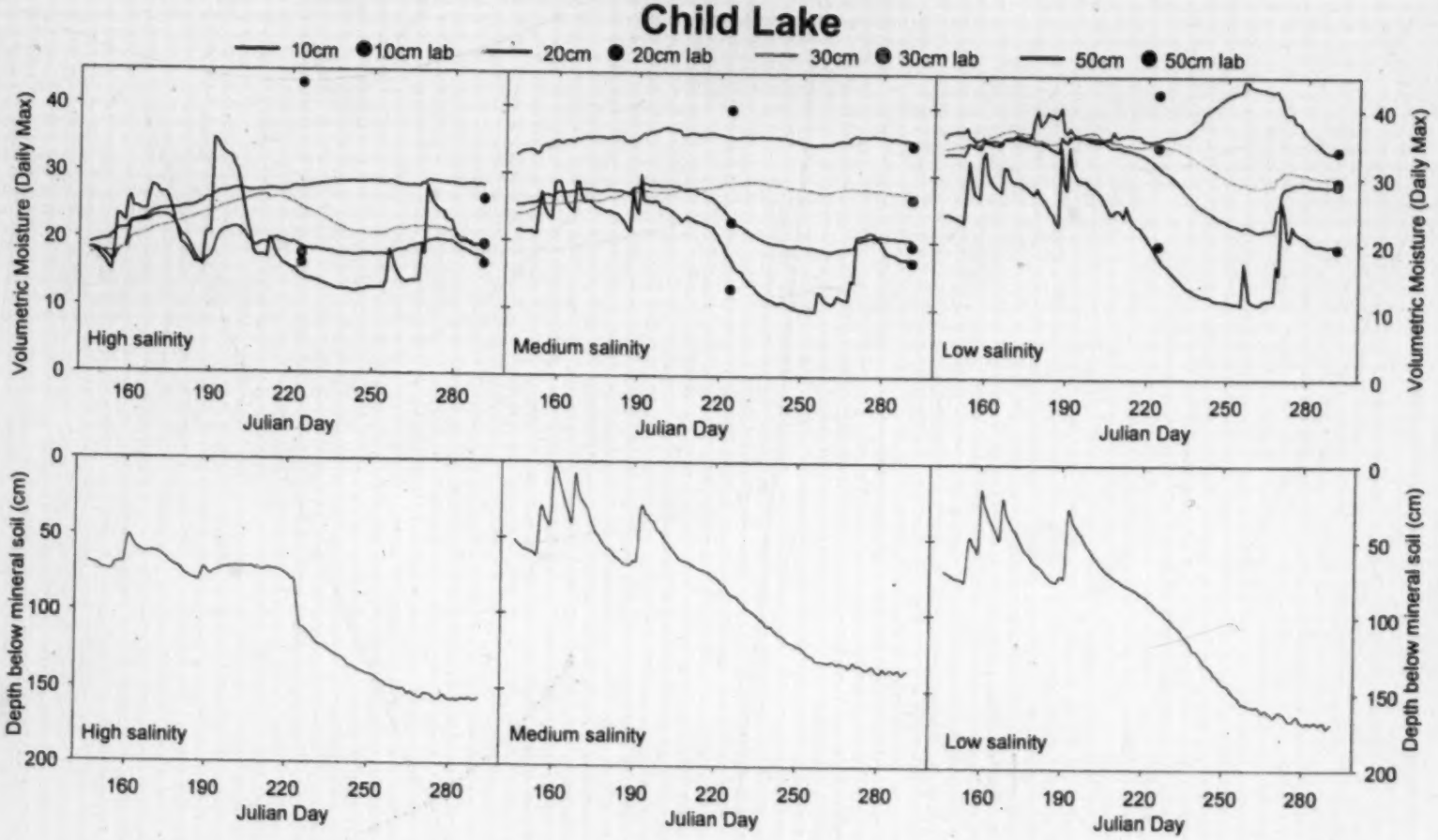
Appendix F. Topographic position of high (H), medium (M), and low (L) salinity plots and the forest edge (triangle) in relation to the nearest standing water for the study areas. Water table level in 2006 is indicated by inverted triangles: mean (black) and minimum and maximum (gray). Bedrock is indicated with "R".

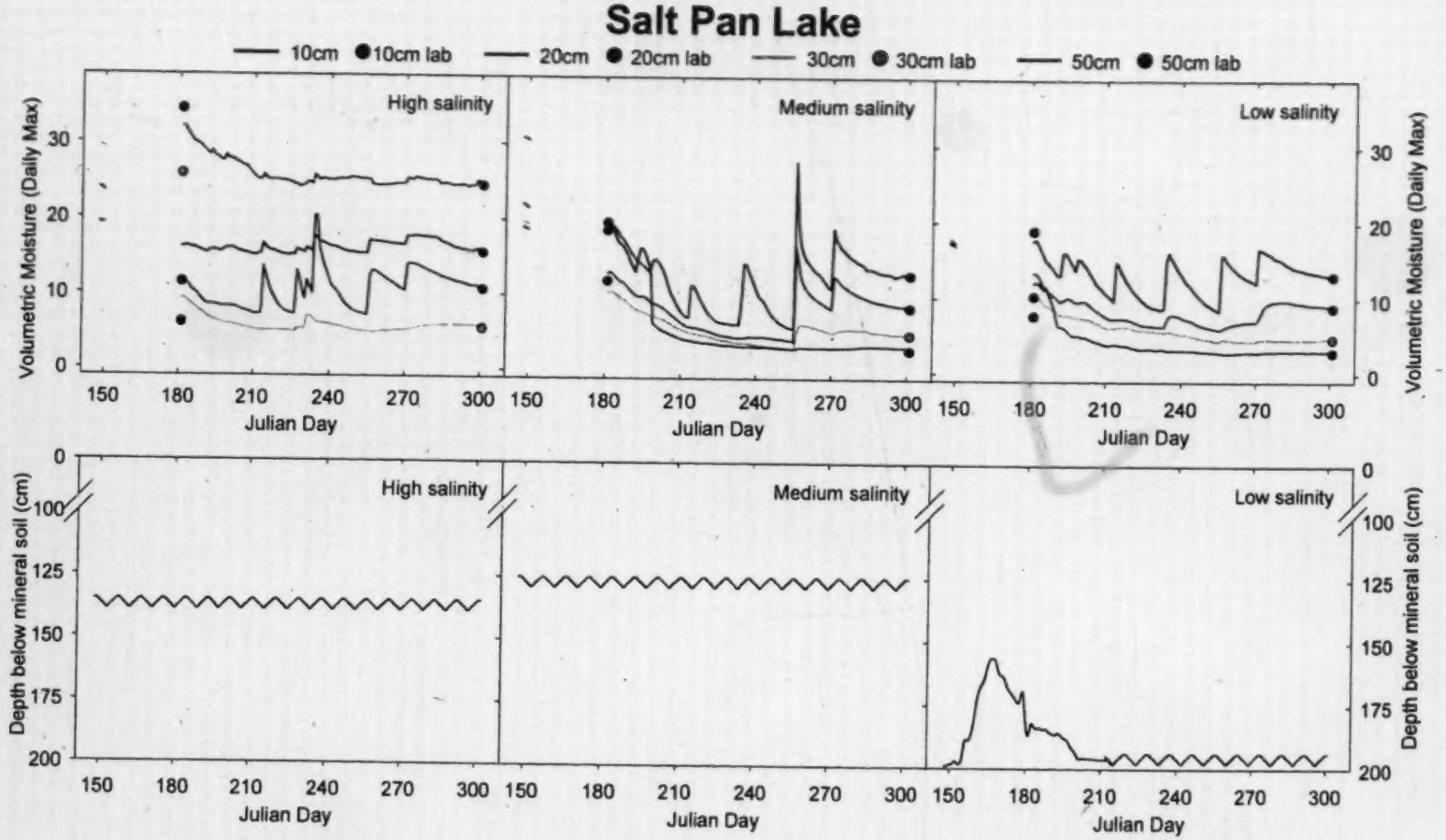


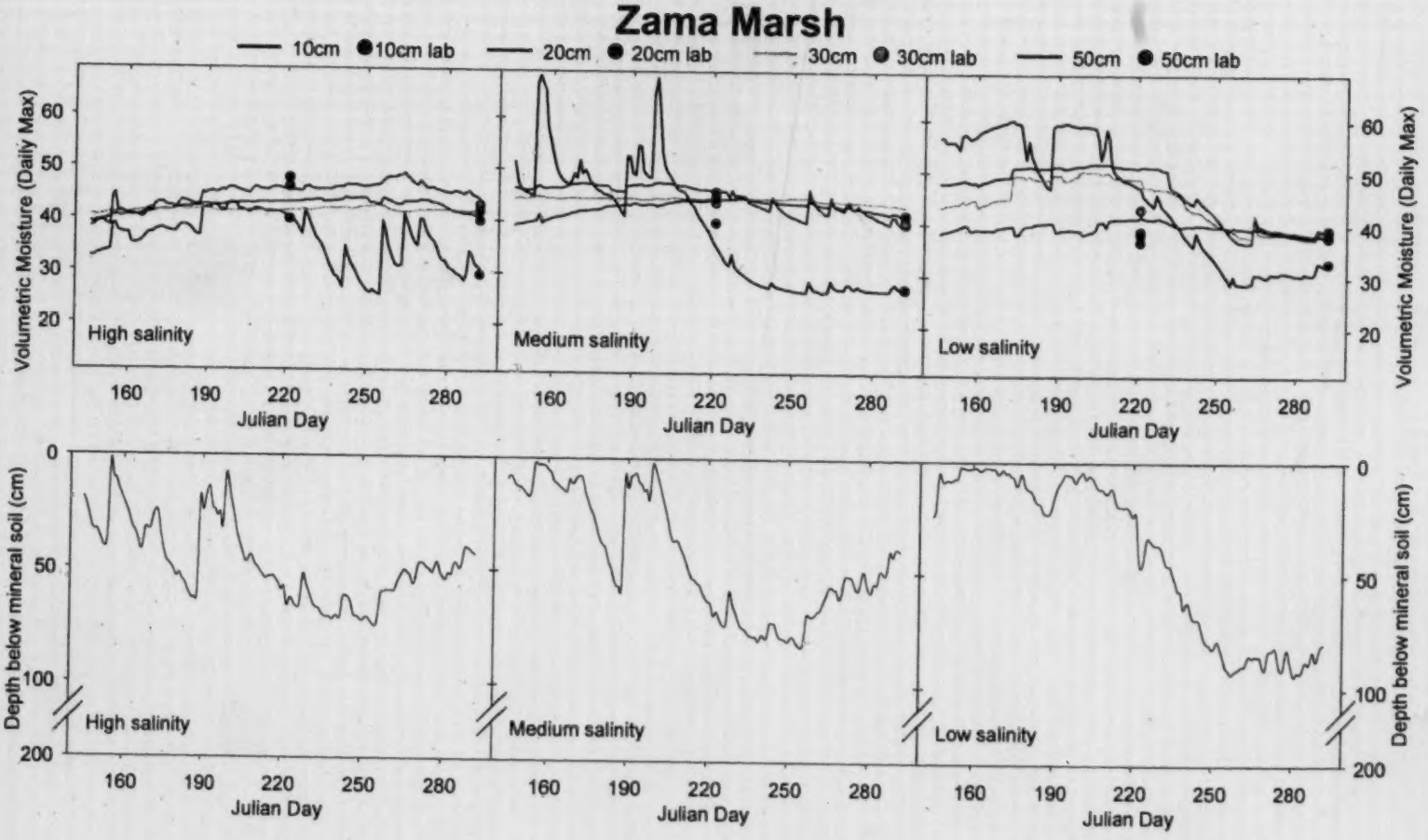
Appendix G. Soil moisture content readings from EasyAg probes and water table level readings from Odyssey probes during the 2006 growing season at high (H), medium (M), and low (L) salinity plots at the study sites. Bedrock is identified with a wavy burgundy line. Circles indicate lab measurements of volumetric moisture used to calibrate the EasyAg probe readings; the first samples were taken midseason from within 10 m of the EasyAg probes and the second samples were taken from within 5 cm of each probe sensor when they were removed at the end of the season.

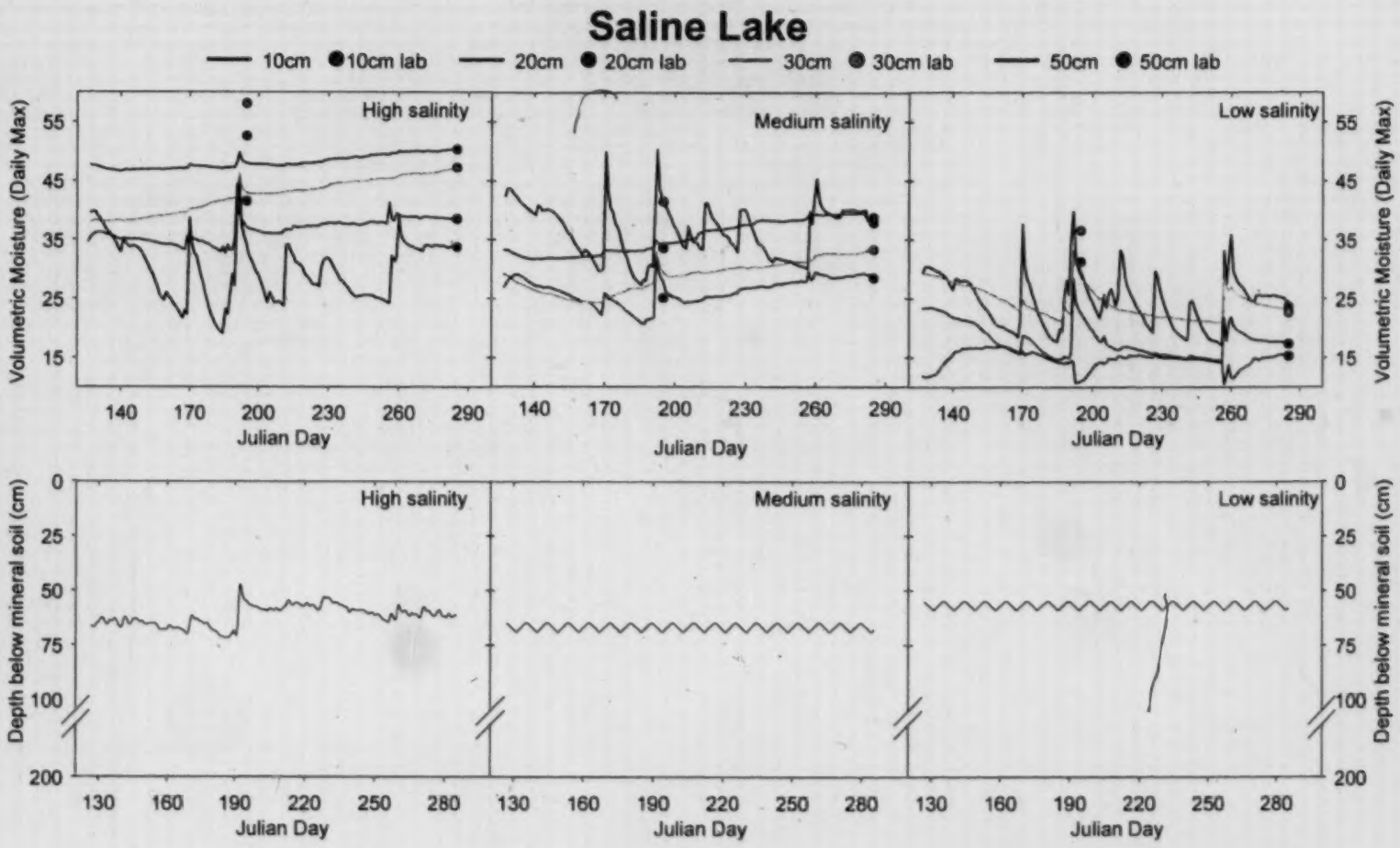



Salt Plains
10cm
10cm lab
20cm
20cm lab
30cm
30cm lab
50cm
50cm lab
High salinity
Medium salinity
Low salinity
Volumetric Moisture (Daily Max)
Depth below mineral soil (cm)
Julian Day
55
45
35
25
15
0
75
100
125
150
175
200
150
180
210
240
270
300


Child Lake
10cm
10cm lab
20cm
20cm lab
30cm
30cm lab
50cm
50cm lab
Volumetric Moisture (Daily Max)
High salinity
Medium salinity
Low salinity
Julian Day
Depth below mineral soil (cm)


Salt Pan Lake
10cm
10cm lab
20cm
20cm lab
30cm
30cm lab
50cm
50cm lab
High salinity
Medium salinity
Low salinity
Volumetric Moisture (Daily Max)
Depth below mineral soil (cm)
Julian Day
0
10
20
30
100
125
150
175
200
150
180
210
240
270
300

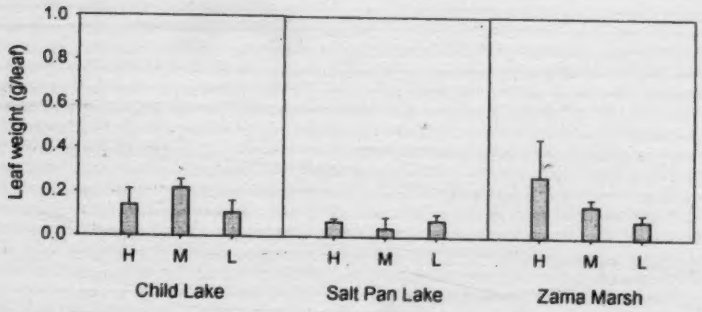

Zama Marsh
10cm
10cm lab
20cm
20cm lab
30cm
30cm lab
50cm
50cm lab
Volumetric Moisture (Daily Max)
High salinity
Medium salinity
Low salinity
Julian Day
Depth below mineral soil (cm)


Saline Lake
10cm
10cm lab
20cm
20cm lab
30cm
30cm lab
50cm
50cm lab
High salinity
Medium salinity
Low salinity
Volumetric Moisture (Daily Max)
Julian Day
Depth below mineral soil (cm)

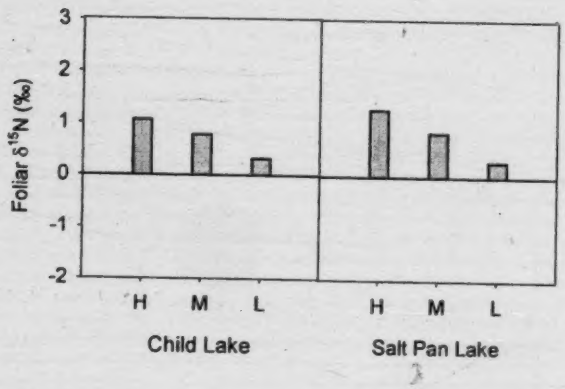
Appendix H. Aspen foliar elemental concentrations (mean ± 95% confidence interval) and stable isotope ratios in high (H), medium (M), and low (L) salinity plots. Units are mg/g except for C and N (%) and stable isotope ratios (‰).

	Child Lake			Salt Pan Lake			Zama Marsh		
Variable	H	M	L	H	M	L	H	M	L
Na	0.20 (0.10)	0.15 (0.05)	0.14 (0.15)	0.12 (0.11)	0.24 (0.06)	0.25 (0.14)	0.31 (0.06)	0.33 (0.08)	0.35 (0.15)
Cl	2.5 (1.1)	2.5 (0.3)	2.6 (2.0)	2.6 (0.8)	1.0 (0.7)	0.9 (0.4)	1.4 (0.8)	2.5 (0.6)	7.4 (2.6)
C	48 (7)	45 (1)	44 (3)	47 (4)	47 (4)	46 (2)	47 (4)	46 (2)	51 (7)
N	2.0 (0.2)	1.8 (0.1)	1.7 (0.4)	2.1 (0.0)	3.1 (0.8)	1.9 (0.3)	2.3 (0.5)	2.2 (0.2)	1.8 (0.2)
P	1.6 (0.4)	1.8 (0.3)	2.3 (0.9)	1.5 (0.1)	3.4 (1.9)	1.7 (0.3)	2.3 (0.6)	1.8 (0.2)	2.1 (0.3)
K	8.0 (2.7)	10.1 (1.2)	9.3 (3.1)	11.0 (0.7)	16.5 (8.5)	11.4 (1.6)	8.6 (3.5)	10.6 (1.0)	14.5 (5.5)
Ca	18 (6)	15 (2)	17 (8)	15 (1)	10 (12)	13 (4)	11 (7)	8.9 (1.4)	11 (1)
Mg	3.2 (1.0)	2.7 (0.3)	4.1 (2.6)	3.2 (0.3)	2.8 (1.1)	2.7 (0.7)	3.9 (1.7)	5.1 (0.7)	4.7 (0.5)
S	1.7 (0.4)	2.0 (0.3)	2.2 (0.3)	2.1 (0.1)	2.5 (0.4)	1.6 (0.2)	2.7 (0.6)	3.8 (0.5)	2.6 (1.3)
Mn	0.13 (0.03)	0.08 (0.01)	0.10 (0.08)	0.11 (0.01)	0.05 (0.06)	0.07 (0.02)	0.12 (0.08)	0.15 (0.05)	0.17 (0.05)
Fe	0.090 (0.012)	0.071 (0.006)	0.066 (0.013)	0.147 (0.258)	0.062 (0.011)	0.067 (0.025)	0.076 (0.013)	0.075 (0.008)	0.086 (0.020)
Al	0.071 (0.010)	0.046 (0.030)	0.051 (0.011)	0.012 (0.019)	0.019 (0.015)	0.030 (0.021)	0.068 (0.036)	0.056 (0.023)	0.060 (0.008)
Zn	0.099 (0.028)	0.169 (0.046)	0.126 (0.159)	0.085 (0.020)	0.086 (0.050)	0.086 (0.016)	0.135 (0.150)	0.083 (0.031)	0.112 (0.022)
Cu	0.018 (0.012)	0.019 (0.014)	0.022 (0.011)	0.013 (0.002)	0.019 (0.002)	0.017 (0.004)	0.024 (0.007)	0.018 (0.004)	0.022 (0.007)
δC13	-26.8 (0.6)	-26.8 (0.2)	-27.1 (1.1)	-27.1 (0.3)	-27.1 (0.4)	-27.2 (0.3)	-26.3 (0.7)	-26.5 (0.7)	-26.9 (0.8)
δN15	1.0 (0.3)	-0.5 (0.1)	1.0 (1.8)	1.5 (0.2)	-0.2 (0.2)	-0.3 (0.5)	1.5 (0.7)	-0.8 (0.6)	-0.6 (0.5)

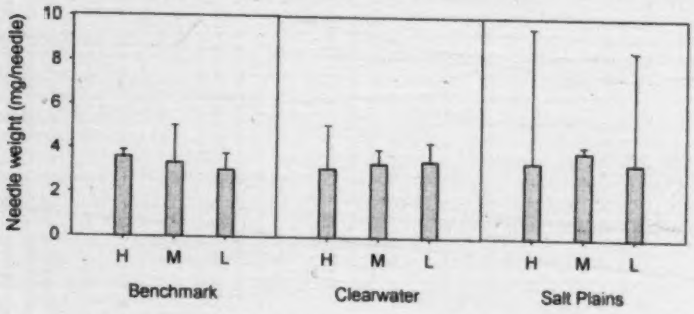
Appendix I. Mean leaf weight and 95% confidence interval for aspen in high (H), medium (M), and low (L) salinity plots.



Appendix J. Foliar $\delta^{15}N$ values from a mixture of aspen leaves collected in 2004 from two felled trees per high (H), medium (M), and low (L) salinity plot. In general, foliage was more enriched in ^{15}N in 2004 – a drier year – compared to 2006 – a wetter year (Figure 3.6).



Appendix K. Means (±95% confidence interval) for white spruce foliar elemental concentrations and stable isotope ratios in high, medium, and low salinity plots. Nutrients are in mg/g except for C and N (%) and stable isotope ratios (‰).

Variable	Benchmark			Clearwater			Salt Plains		
	H	M	L	H	M	L	H	M	L
Na	0.20 (0.14)	0.22 (0.07)	0.21 (0.06)	0.28 (0.35)	0.64 (1.36)	0.18 (0.05)	0.26 (0.85)	0.18 (0.04)	0.27 (0.09)
Cl	0.25 (0.23)	0.18 (0.08)	0.20 (0.12)	0.20 (0.10)	0.24 (0.14)	0.20 (0.06)	0.20 (1.04)	0.24 (1.00)	0.25 (0.13)
C	49 (3)	49 (4)	47 (5)	48 (2)	48 (2)	47 (2)	47 (4)	46 (54)	48 (9)
N	0.7 (0.2)	0.8 (0.2)	0.9 (0.3)	1.0 (0.2)	1.1 (0.2)	0.9 (0.0)	1.0 (0.1)	1.1 (0.1)	1.1 (0.7)
P	1.0 (0.4)	1.5 (0.9)	1.4 (0.8)	1.3 (0.6)	1.4 (0.2)	1.3 (0.3)	1.2 (0.4)	1.4 (0.7)	1.7 (0.9)
K	5.3 (3.3)	6.5 (3.3)	6.3 (4.3)	5.3 (1.6)	6.2 (1.5)	4.7 (1.2)	7.3 (3.3)	6.6 (3.8)	7.1 (8.2)
Ca	8.0 (3.7)	11.0 (7.2)	7.2 (2.7)	13.4 (5.2)	12.4 (2.7)	13.6 (10.7)	11.3 (9.9)	20.7 (18.7)	17.0 (18.8)
Mg	1.1 (0.6)	1.1 (0.6)	0.9 (0.4)	1.0 (0.4)	1.0 (0.4)	1.3 (0.3)	0.8 (0.2)	0.7 (1.7)	1.2 (0.4)
S	0.6 (0.2)	0.9 (0.5)	0.8 (0.3)	0.9 (0.2)	1.0 (0.2)	0.9 (0.1)	0.9 (1.2)	1.0 (0.0)	0.9 (0.2)
Mn	0.5 (0.4)	1.0 (0.9)	0.6 (0.3)	0.3 (0.3)	0.3 (0.2)	0.3 (0.1)	0.1 (0.6)	0.4 (0.4)	0.3 (0.5)
Fe	0.04 (0.02)	0.05 (0.02)	0.05 (0.01)	0.05 (0.01)	0.05 (0.02)	0.05 (0.02)	0.06 (0.06)	0.08 (0.16)	0.08 (0.04)
Al	0.06 (0.02)	0.06 (0.05)	0.07 (0.03)	0.04 (0.04)	0.03 (0.03)	0.03 (0.02)	0.03 (0.01)	0.06 (0.03)	0.06 (0.04)
Zn	0.05 (0.02)	0.08 (0.06)	0.05 (0.01)	0.09 (0.04)	0.08 (0.04)	0.07 (0.03)	0.09 (0.08)	0.11 (0.08)	0.11 (0.16)
Cu	0.018 (0.004)	0.020 (0.013)	0.014 (0.005)	0.013 (0.008)	0.007 (0.004)	0.012 (0.008)	0.013 (0.016)	0.012 (0.053)	0.037 (0.058)
$\delta^{13}C$	-26.0 (0.9)	-26.4 (1.0)	-26.0 (0.8)	-26.4 (0.5)	-26.3 (0.7)	-26.4 (0.6)	-25.9 (2.4)	-26.4 (0.2)	-26.6 (0.9)
$\delta^{15}N$	-2.8 (1.2)	-2.3 (0.2)	-0.7 (0.8)	-1.6 (0.6)	-1.1 (1.9)	-2.2 (1.4)	-1.3 (4.1)	-1.1 (6.4)	-1.1 (3.1)

Appendix L. Mean weight per needle (and 95% confidence intervals) for white spruce needles in high (H), medium (M), and low (L) salinity plots at each of the three sites. Needles were collected from 4 trees per plot at Benchmark and Clearwater, but from only 2 (high and medium salinity plots) or 3 (low salinity plot) trees per plot at Salt Plains.